

RECORDS
OF
THE
SOUTH
AUSTRALIAN
MUSEUM

VOLUME 30 PART 1
JULY 1997

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Summary

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SOUTHCOTT, R. V. 1997. Description of two new larval Smarididae (Acarina) from Australia. *Records of the South Australian Museum* 30(1): 1–12.

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The mite family Smarididae Vitzthum, 1929 is cosmopolitan, most members being known as adults. The adults (and deutonymphs) are small mites, of a generally flattened stature, living as predators in litter or under the bark of trees. These mites are mostly known from their adult instars. The larvae are probably all ectoparasitic on small arthropods, as is the case with most other members of the superfamily Erythraeoidea. Thus one Australian larva, *Smaris prominens* (Banks, 1916), has been found as an ectoparasite of small Psocoptera (Womersley & Southcott 1941). A taxonomic and historical review of the family was given by Southcott (1961a). Seven genera are known as larvae (Southcott 1995). Of these two are Australian, each with a single described species; that of *Smaris prominens* (Banks, 1916) (by Womersley & Southcott 1941), and of *Sphaerotarsus leptopilus* Womersley & Southcott, 1941 (by Southcott 1960). The present paper describes a further new species in each of these genera, both from South Australia, and known only as larvae.

Leitz Ortholux/Laborlux microscope equipped with phase contrast and polarizing facilities. Drawings were made with the use of a drawing apparatus.

Chaetotaxic and other nomenclature and coding are as in Southcott (1961b, c, 1963, 1992, 1995). The code AME is introduced as a measure of the anterior central emargination of the dorsal scutum. (In my previous papers I had misinterpreted the use of this term as ASBM, which was introduced by Fain & Elsen 1987). AME may be formally defined as the distance between the anterior end of the scutum, in the midline, to the central anterior point of the scutum; hence $AME = ASBa - ASBM$ (Fain & Elsen).

The terms protorostral, deutorostral and tritorostral will be used for the anterior setae of the gnathosoma, following Newell (1957).

All measurements are in micrometres (μm) unless otherwise stated.

All specimens will be deposited in the South Australian Museum (SAM).

MATERIALS AND METHODS

Specimens described in this paper were obtained by Berlese funnel extractions of samples of soil and litter in South Australia. They were collected as active larvae, and each was confined individually in a small tube and various small arthropods were introduced as potential hosts, in an effort to elucidate life histories.

The larvae were eventually mounted in Hoyer's medium after first being cleared in 50% lactic acid solution. Microscopy was done with the use of

SYSTEMATICS

Family SMARIDIDAE Vitzthum

Smarididae Vitzthum, 1929: 69, 70; Womersley & Southcott 1941: 61; Southcott 1946: 173; 1948: 252; 1960: 149; 1961a: 174; 1961b: 413; 1961c: 133; 1963: 159; 1995: 57; Shiba 1976: 189.

Erythraeidae Womersley, 1934: 218 (part).

Smarisidae Grandjean, 1947: 1.

For other synonymy see Southcott 1961b: 413–414.

Genus *Smaris* Latreille

Smaris Latreille, 1796: 180; Womersley & Southcott 1941: 63; Southcott 1946:175; 1948: 252; 1960: 155; 1961a: 176–177; 1961b: 438; 1961c: 133; 1963: 163; 1995: 63.

Sclerosmaris Grandjean, 1947: 3, 53.

For other synonymy see Southcott 1961b: 438–439.

KEY TO LARVAL *SMARIS*

- PDS 27–29 μm long. AL scutalae blunt-ended. Sternala I thickened, well setulose *S. prominens* (Banks, 1916)
- PDS 28–45 μm long. AL scutalae pointed. Sternala I narrow, lightly setulose *S. arenicola* sp. nov.

Smaris arenicola sp. nov.
(Figs 1A–D, 2A,B)

Material examined

Holotype. South Australia: Loveday, 7–8.ix.1985, R. V. Southcott, larva ACA2158 from soil and litter sample TX244, site Map: Department of Lands, South Australia, Barmera-Loveday, 2nd Edition 1:10,000 6929–26, MR 466055 (140°25'03"E, 34°17'25"S), extracted by Berlese funnel live 6.x.1985; to Hoyer's medium 28.i.1991. SAM.

Paratypes. Same data as holotype, 21 larvae from same site and sample, ACA2150, 2152–2156, 2159–2173, extracted live similarly 24.ix.1985–10.x.1985; Hoyer's medium. SAM.

Diagnosis of larva

Anterior scutalae pointed. GeIII 65–72 μm long. PDS 28–45 μm long.

Description of larva (from slide-mounted holotype, supplemented by paratypes)

Colour in life red. Idiosoma 245 long, 180 wide; total length of animal 330.

Dorsal scutum transverse, oval, with slight central anterior emargination, minutely porose. Scutalae slender, pigmented, AL pointed, PL blunt-ended, with adnate to slightly outstanding setules. AL scutalae placed anterolaterally on scutum; PL placed posterolaterally; all near edge of scutum. Anterior sensillary setae placed about midway between levels of AL and PL scutalae bases; sockets of posterior sensillary setae lightly

protruding, placed at about middle of posterior border of scutum. Anterior sensillary setae thin, but thicker than the filamentous posterior sensillary setae; all with slight setules in distal two-thirds, longer distally.

Metric data as in Table I.

Dorsal idiosomal setae about 41 in number, pigmented, blunt-ended, with short, barbed setules; anterior setae in indistinct rows across dorsum; posterior setae form a denser group.

Ventral surface of idiosoma: two sternalae between coxae I, pigmented, pointed, lightly setulose; sternalae II vestigial, presenting as small domes *c.* 5 across, between coxae II; between coxae III two intercoxalae 28 long, similar to sternalae I. Behind coxae III *c.* 11 setae similar to dorsals, 27–36 long, arranged approximately 2, 4, 4, 1, with a denser grouping towards posterior pole.

Legs fairly short and thick, similar to those of *Smaris prominens* (see Womersley & Southcott 1941); lengths (including coxae and claws): I 380, II 370, III 410. Coxalae and other leg scobalae pigmented, setulose, pointed. Supracoxala to leg I a slender, blunted peg, 5 long.

Leg specialized setae: SoGeI.77pd(23), VsGeI.90pd(4), SoTiI.50d(38), SoTiI.70pd(33), CpTi.75d(8)+SoTiI.76d(28), SoTiI.78d(12), VsTiI.83pd(6), SoGeII.51pd(15), SoTiII.03d(16), SoTiII.78d(10), SoGeIII.52d(14), SoTiIII.03d(12).

Tarsus I with SoTaI.37d(45), curved, strong, pointed; FaTaI.40ad(6); tarsus I also with an accompanying trichobothria to the solenoidala, with several long setules, at .44d, seta 40 long. Tarsus II with SoTaII.35d(18), slender, nearly recumbent. FaTaII appears as a minute vestigial structure immediately alongside, i.e. posterior to, SoTaII. All tarsi with a long, slender, blade-like empodium, 23–27 long, over-reaching lateral claws, which are paired on each tarsus, about 18 long, each a pad with a number of long ventral onychotrichs.

Gnathosoma robust, pyriform, 77 long by 75 wide (combined). Cheliceral digits S-shaped, 16 long, sharp-pointed. Protorostral (galeal) seta simple, slender, pointed, 14 long. Deutorostral seta simple, conical, 7 long. Tritorostral setae simple, slender, pointed, 21 long. Palpal setal formula 0, 0, 1, 1, 3, 7 (including solenoidala and terminala (eupathidala)); all setae (except palptarsal solenoidala) pointed; femorala, genuala and tibialae 1 and 2 setulose. Odontus pointed, hook-like, with two dorsal supplementary spurs behind tip. Palpal supracoxala dorsal in position, a clavate rod 5 long.

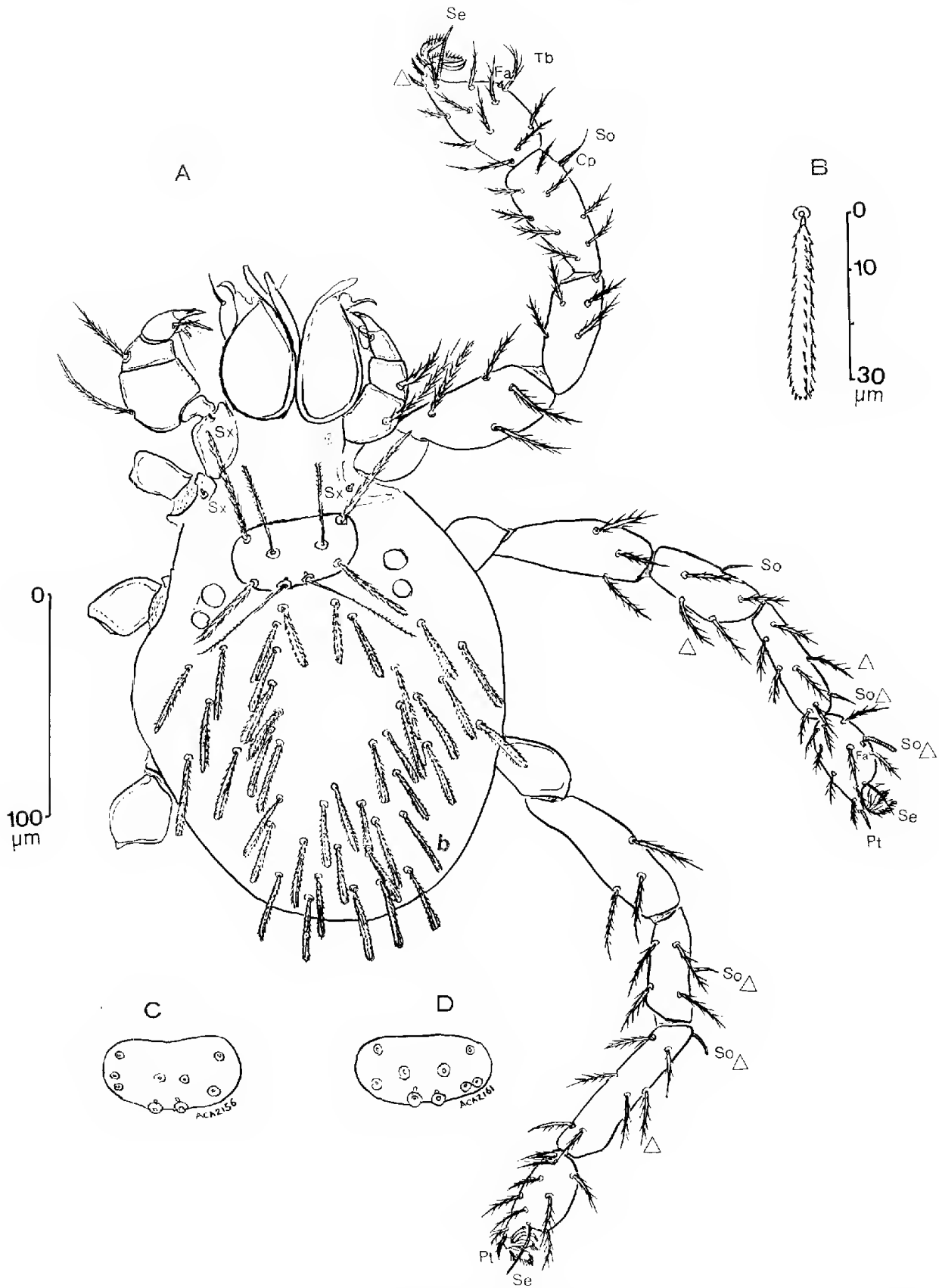


FIGURE 1. *Smaris arenicola* sp. nov., larva. A, B holotype; A, Dorsal view, on left legs omitted beyond trochanters; B, Dorsal idiosomal seta ('b' in A). C, D Paratypes: C, Teratological dorsal scutum of ACA2156; D, teratological dorsal scutum of ACA2161. (Each to nearest scale.)

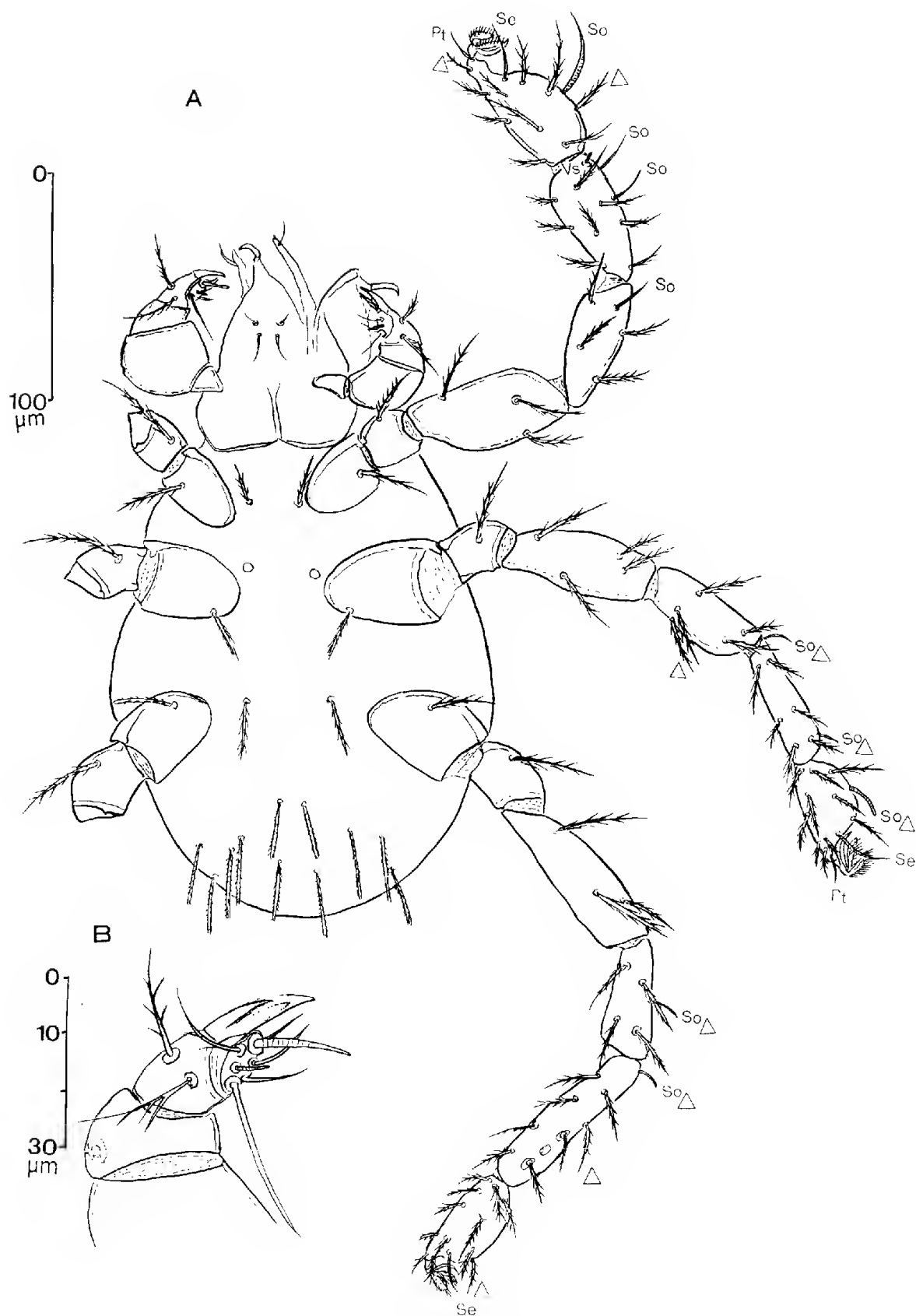


FIGURE 2. *Smaris arenicola* sp. nov., larva, holotype. **A**, Ventral view, on left legs omitted beyond trochanters. **B**, Tip of palp, ventral view, further enlarged.

TABLE 1. Metric data for *Smaris arenicola* sp. nov. larvae (*for maximum values)

Character	Holotype	n	range	mean	s.d.	c.v.
AW	47	22	43–49	45.5	1.37	3.0
PW	50	22	42–53	48.3	2.35	4.9
SBa	22	21	19–23	22.1	1.01	4.6
SBp	16	21	13–16	15.0	0.921	6.1
LX	8	21	6–12	8.81	1.21	13.7
ASBa	20	21	15–22	17.8	1.83	10.3
AME	2	21	1–3	2.10	0.436	20.8
ISD	15	21	14–17	15.0	0.805	5.4
L	38	21	34–39	35.8	1.34	3.7
W	63	21	58–72	63.7	3.44	5.4
AAS	16	21	14–16	15.1	0.831	5.5
A–P	20	21	15–20	16.9	1.64	9.7
AL	56	21	45–64	55.1	3.54	6.4
PL	43	22	36–47	42.1	2.83	6.7
ASE	40	21	36–44	39.7	1.93	4.9
PSE	65	19	60–73	66.2	3.92	5.9
DS	31–38	22	38–45*	41.0*	1.79*	4.4*
'Oc.'	37	22	36–42	38.1	1.98	5.2
MDS	32	22	32–38	34.4	1.99	5.8
PDS	31–38	22	38–45*	40.8*	2.05*	5.0*
Gel	68	22	60–69	64.7	1.93	3.0
Til	66	22	60–69	64.7	2.12	3.3
Tal(L)	68	22	64–73	68.5	2.39	3.5
Tal(II)	33	22	27–35	32.2	2.56	7.9
Til/Gel	0.97	22	0.92–1.07	1.00	0.0340	3.4
GelI	62	22	55–64	59.3	2.44	4.1
TilI	66	22	62–68	65.6	1.89	2.9
TalI(L)	50	22	47–60	52.8	3.15	6.0
TalI(H)	27	22	20–31	26.4	3.06	11.6
TilI/GelI	1.06	22	1.02–1.19	1.11	0.0490	4.4
GelII	68	22	65–72	67.9	1.77	2.6
TilII	93	22	86–93	89.9	2.04	2.3
TalII(L)	55	22	49–61	56.3	2.64	4.7
TalII(H)	26	22	20–29	25.0	2.29	9.2
TilII/GelII	1.37	22	1.28–1.38	1.32	0.0360	2.7
AW/ISD	3.13	21	2.75–3.36	3.04	0.187	6.1
ISD/A–P	0.75	21	0.75–1.07	0.887	0.0913	10.3
AW/A P	2.35	21	2.15–3.00	2.71	0.260	9.6
StI	18	22	18–29	22.4	2.97	13.3
CxI	42	22	40–53	44.0	2.59	5.9
CxII	22	21	20–31	23.3	2.51	10.8
CxIII	31	21	26–36	32.1	2.78	8.6
Til/AW	1.40	22	1.32–1.56	1.42	0.0668	4.7
TilII/AW	1.98	22	1.83–2.12	1.98	0.0666	3.4
AW/AL	0.84	21	0.70–1.02	0.829	0.0599	7.2
AL/AAS	3.50	20	2.81–4.27	3.65	0.341	9.3
TilII/Til	1.41	22	1.28–1.44	1.39	0.0402	2.9
TilII/PW	1.32	22	1.22–1.57	1.36	0.0768	5.6
L/W	0.60	21	0.47–0.64	0.56	0.0416	7.4
PW/AW	1.06	22	0.93–1.18	1.06	0.0545	5.1
AL/PL	1.30	21	1.13–1.52	1.31	0.112	8.5

Etymology

The specific epithet *arenicola* means 'sand-dwelling' (Latin), a reference to the site of capture.

Biology

All larvae were captured free. In an attempt to find possible hosts larvae were introduced individually into small tubes, and various small arthropods introduced as potential hosts. These included various insects: small moths, small hemipterans (aphids, psyllids, a ?mirid), small Diptera and wingless Psocoptera; also a small spiderling. However, no attempt at parasitization by any of the mites was observed.

Genus *Sphaerotarsus* Womersley

Sphaerotarsus Womersley, 1936: 119; Womersley & Southcott 1941: 63, 73; Southcott 1960: 149; 1961a: 177; 1961b: 144; 1963: 211; 1995: 57, 63.

Definition of larva

One eye on each side. Anterior sensillary bases anterior to AL scutalae bases; posterior sensillary bases posterior to PL scutalae bases. Palpal tibial claw (odontus) apically simple or with narrow terminal split, and an outstanding basal accessory tooth. Genu I with 3–6 solenoidae. Tibia I with four solenoidae.

KEY TO LARVAL *SPHAEROTARSUS*

- PDS to 127 µm long
.. *S. leptopilus* Womersley & Southcott, 1941
- PDS to 86 µm long *S. monticolus* sp. nov.

Sphaerotarsus monticolus sp. nov.

(Figs. 3A,B, 4A,B)

Material examined

Holotype. South Australia. Mt. Lofty, 5-20.x.1991, R. V. Southcott, larva ACA2556, in damp soil and litter in *Eucalyptus obliqua* forest, sample TX320, site at Map: Adelaide 6628-111, 1:50,000, MR 897282 (138°41'47" E., 34°58'03" S.), sample collected 5.x.1991, extracted live by Berlese funnel 20.x.1991. Cleared with 50% lactic acid, mounted in Hoyer's medium.

Paratypes. South Australia. Hope Forest, 11.ix.1980, RVS, in moss under *Eucalyptus baxteri* forest, at Map Reference Milang 1:63,360 617393 (138°36'19"E., 35°18'06"S.), site TX198,

extracted by Berlese funnel 14-23.ix.1980. Stirling, at Map Reference Adelaide 1:50,000, 2nd Edn., 934258 (138°44'0"E., 34°59'30"S.), 11.xi.1984, RVS, sample TX232 of soil, litter and grass under *Eucalyptus hueberiana*, extracted by Berlese funnel 17.xi.1984.

Diagnosis of larva

PDS to 66 µm long.

Description of larva (from slide-mounted holotype)

Colour in life: idiosoma orange, legs pale orange. Idiosoma 325 long, 220 wide. Total length to tip of cheliceral digits 410; in life these dimensions were 300, 200, 380 respectively.

Dorsal scutum trapezoidal, with rounded anterior end and acute posterior end; scutum minutely porose. Scutum has a sclerotized ridge enclosing the anterior and posterior sensillary areas, of a tear-drop shape, the point posteriorad, and within the bases of the four scutalae. Scutalae pointed, with many fine, pointed setules. Anterior sensillary setae thicker than the filamentous posterior sensillary setae; all sensillary setae with fine setules in distal half of setal shaft.

Metric data as in Table 2.

Eyes 1+1, lateral to scutum, 18 across.

Dorsum of idiosoma with 24 setae, pigmented, expanding slightly distally, blunt-ended, with many fine setules; setae arranged approximately 6, 4, 2, 4, 2, 4, 2.

Ventral surface of idiosoma: sternalae I pointed, setulose; sternalae II absent; anterior to coxae III a pair of intercoxalae similar to sternalae I, 36 long, 60 apart. Behind coxae III are 10 pointed, setulose setae, arranged 4, 2, 2, 2.

Legs somewhat longer than idiosoma; lengths (including coxae and claws): I 400, II 395, III 495. Leg scobalae pointed, lightly setulose. Supracoxala to leg I blunted, 4 long.

Leg specialized setae: TbGeI.44ad(25), TbGeI.44pd(22), SoGeI.60pd(23), SoGeI.67d(16), SoGeI.76pd(17), VsGeI.90d(3), TbTiI.48pd(28), TbTiI.53ad(29), TbTiI.54pv(27), TbTiI.54av(29), SoTiI.61pd(30), SoTiI.67d(30), SoTiI.77pd(30), CpTiI.80ad(9)+ScTiI.82ad(30), SoTiI.86d(25), VsTiI.95pd(2), VsGeII.88d(1), SoTiII.11d(14), SoTiII.86d(10), SoTiIII.09d(18).

Tarsus I with SoTaI.17ad(20), TbTaI.20pd(22), CpTaI.40ad(9)+SoTaI.42ad(22), FaTaI.58ad(1), CpTaI.70d(6)+TbTaI.71d(29). Tarsus II with SoTaII.39d(20). Lateral tarsal claws with a few slender onychotrichs; empodium slender, over-reaching lateral claws.

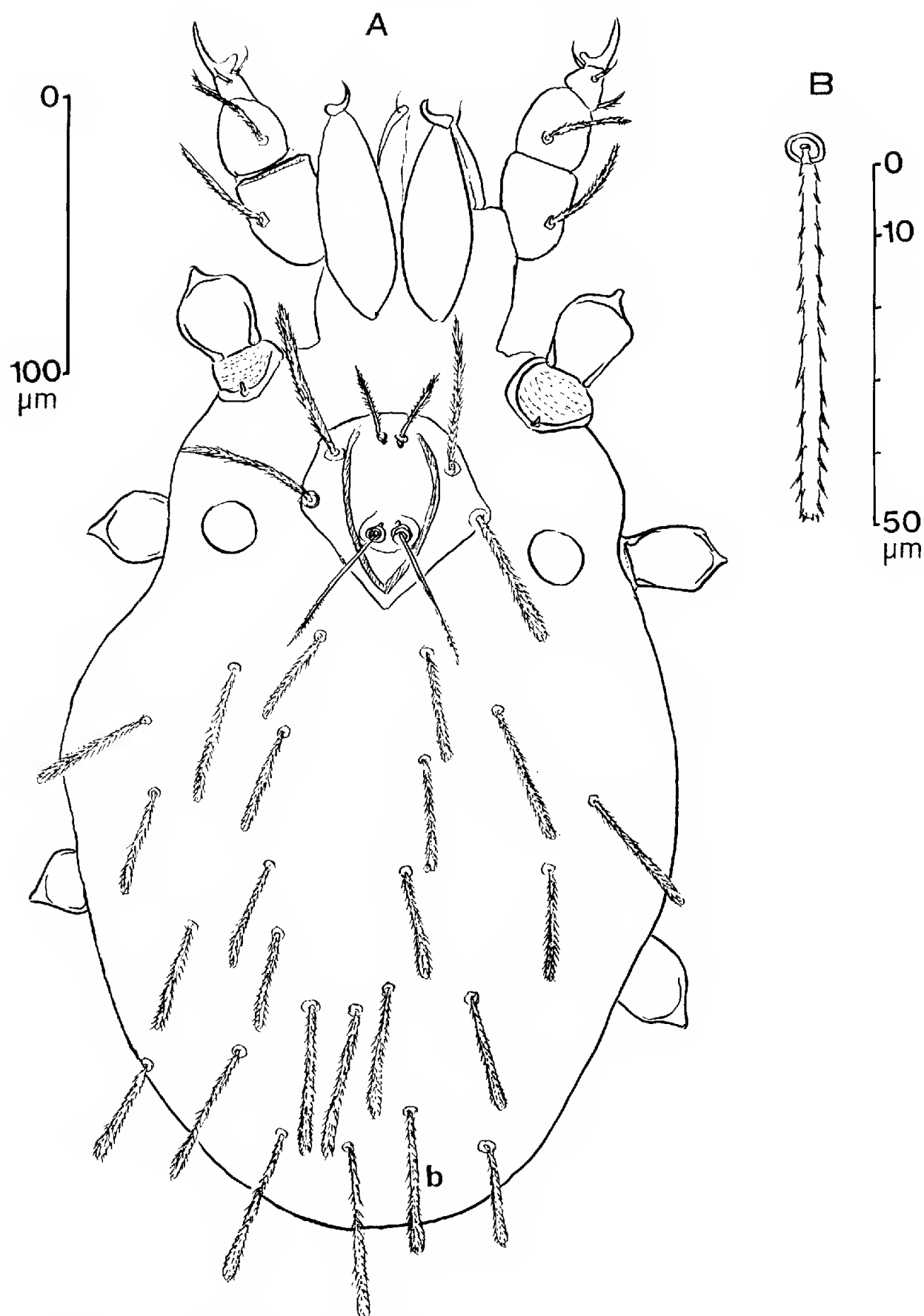


FIGURE 3. *Sphaerotarsus monticolus* sp. nov., larva, holotype. A, Dorsal view, legs omitted beyond trochanters. B, Dorsal idiosomal seta ('b' in A), further enlarged.

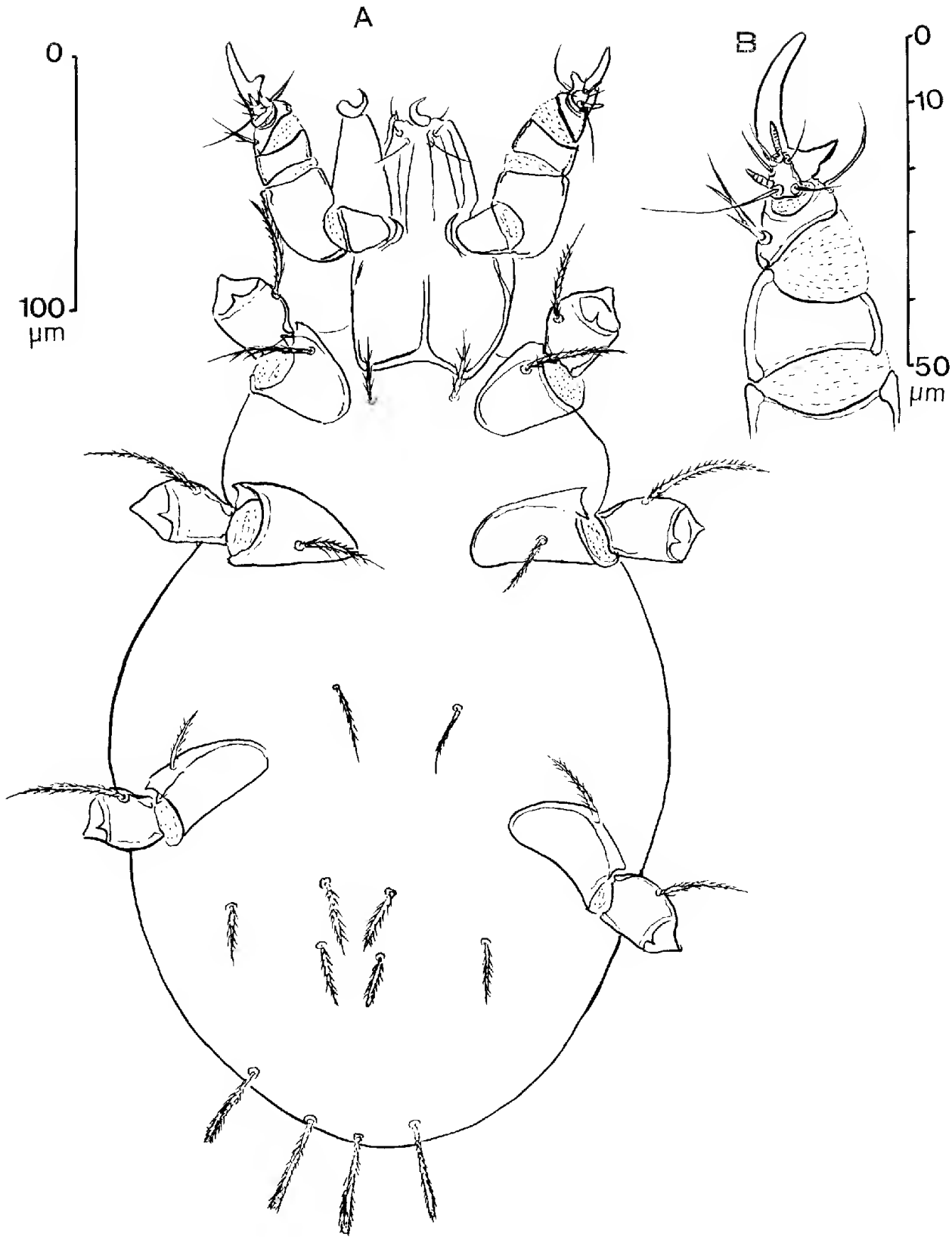


FIGURE 4. *Sphaerotarsus monticolus* sp. nov., larva, holotype. A, Ventral view, legs omitted beyond trochanters. B, Tip of palp, ventral view, further enlarged.

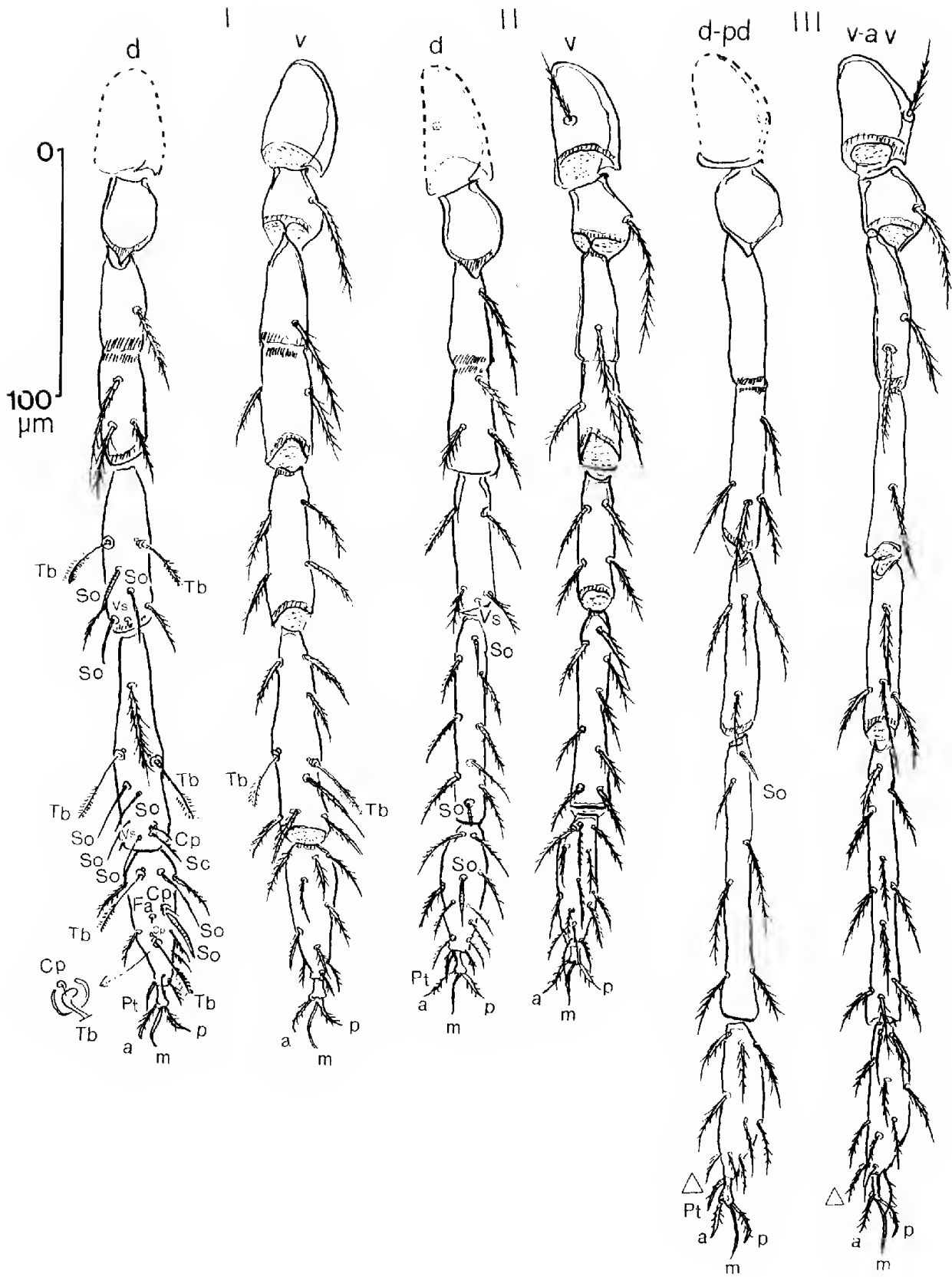


FIGURE 5. *Sphaerotarsus monticolus* sp. nov., larva, holotype. Legs I, II, III. (All to scale shown.)

TABLE 2. Metric data for *Sphaerotarsus monticolus* sp. nov. larvae (*for maximum values)

Character	Holotype	n	range	mean	s.d.	c.v.
AW	43	10	36-47	41.7	2.98	7.2
PW	55	10	47-66	56.8	6.44	11.3
SBa	8	10	6-13	10.6	2.17	20.5
SBp	12	10	11-14	12.2	1.40	11.5
LX	17	10	15-23	20.1	3.00	14.9
ASBa	10	10	9-16	13.4	2.76	20.6
AME	0	10	0-1	0.10	0.316	3.2
ISD	35	10	30-38	34.5	2.99	8.7
L	66	10	63-78	72.1	5.24	7.3
W	64	10	59-75	67.3	6.38	9.5
AAS	19	10	15-22	17.5	2.01	11.5
A-P	19	10	14-30	21.7	5.29	24.4
AL	58	10	57-78	66.6	7.88	11.8
PL	57	10	57-80	67.8	9.26	13.7
ASE	21	10	21-29	25.9	2.85	11.0
PSE	49	10	49-68	57.5	6.43	11.2
DS	42-66	10	55-86*	73.5*	10.5*	14.2*
'Oc.'	45	10	45-73	58.5	9.92	17.0
MDS	45	10	40-73	54.4	11.8	21.8
PDS	66	10	55-86*	73.5*	10.5*	14.2*
GeI	73	10	72-82	76.5	3.37	4.4
TiI	91	10	82-97	89.6	4.93	5.5
TaI(L)	55	10	52-67	60.4	5.19	8.6
TaI(H)	22	10	22-33	27.2	9.15	33.6
TiI/GeI	1.25	10	1.11-1.25	1.16	0.0372	3.2
GeII	60	10	56-85	62.0	4.00	6.5
TiII	85	10	76-86	82.3	4.27	5.2
TaII(L)	52	10	51-60	55.7	3.71	6.7
TaII(H)	18	10	18-26	22.4	2.41	10.8
TiII/GeII	1.02	10	1.02-1.40	1.28	0.107	8.3
GeIII	78	10	72-90	82.0	6.86	8.4
TiIII	124	10	114-140	127.0	8.56	6.7
TaIII(L)	63	10	62-75	66.8	4.54	6.8
TaIII(H)	17	10	17-24	21.5	2.22	10.3
TiIII/GeIII	1.59	10	1.48-1.74	1.56	0.0707	4.5
AW/ISD	1.23	10	1.05-1.67	1.24	0.184	14.9
ISD/A-P	1.84	10	1.20-2.29	1.66	0.340	20.5
AW/A-P	2.26	10	1.54-3.36	2.04	0.596	29.2
StI	34	10	29-35	32.9	1.79	5.4
CxI	49	10	49-62	55.6	4.03	7.3
CxII	37	10	34-48	38.0	4.22	11.1
CxIII	34	10	33-41	37.6	3.57	9.5
TiI/AW	2.12	10	1.81-2.28	2.16	0.184	8.5
TiIII/AW	2.88	10	2.66-3.50	3.08	0.242	7.9
AW/AL	0.74	10	0.51-0.82	0.635	0.0901	14.2
AL/AAS	3.05	10	2.59-4.59	3.85	0.608	15.8
TiIII/TiI	1.36	10	1.36-1.50	1.44	0.0505	3.5
TiII/PW	1.55	10	1.27-1.61	1.43	0.144	10.0
L/W	1.03	10	1.03-1.17	1.07	0.0572	5.3
PW/AW	1.26	10	1.01-1.61	1.40	0.198	14.2
AL/PL	1.02	10	0.88-1.09	0.988	0.0601	6.1

Gnathosoma comparatively slender; cheliceral bascs 64 long by 50 wide (combined); cheliceral blades 16 long, slender, curved, pointed. Protorostral setae simple, pointed, 9 long. Deutorostral setae small, pointed, *c.* 5 long. Tritorostral setae slender, simple, pointed, *c.* 18 long. Palpi fairly robust, with setal pattern 0, 0, 1, 1, 3, 7 including solenoidala and eupathidala (terminala). Palpal femorala and genuala blunt-ended, setulose; palpal tibiala 1 pointed, setulose; palpal tibialae 2 and 3 simple, pointed. Odontus simple, with strong ventral, conical, blunted tooth. Supracoxala not identified.

Etymology

The specific epithet is an adjective, meaning 'mountain dwelling' (Latin).

Biology

Some observations were made on the living

larva ACA2121. On capture it appeared active and healthy; it was identified in life by being weighted down on a slide by a small cover glass, and examined at 400 diameters magnification. After release it became quite active again. It was placed in a small dry tube, and droplets of water given. Various small arthropods recovered from the berlesate were offered as potential hosts over several days: a small coccid (Hemiptera), 7–8 Collembola (?Isotomidae) and an immature psocopteran. However, no attempt at parasitization was observed during the nine days it survived in the tube,

ACKNOWLEDGMENTS

The work was done with the support of a grant from the Australian Biological Resources Study.

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**A NEW SHRIMP OF THE GENUS RHYNCHOCINETES FROM THE
GREAT AUSTRALIAN BIGHT (CRUSTACEA : DECAPODA :
RHYNCHOCINETIDAE)**

JUNJI OKUNO

Summary

A new shrimp of the family Rhynchocinetidae, *Rhynchocinetes enigma*, is described and illustrated on the basis of two males and an ovigerous female from the Great Australian Bight. This species is readily distinguished from the other eleven congeners by the absence of an arthrobranch from the third maxilliped or lack of an arthrobranch on the pereopods. It represents the fourth rhynchocinetid species from depths exceeding 100 m.

A NEW SHRIMP OF THE GENUS *RHYNCHOCINETES* FROM THE GREAT AUSTRALIAN BIGHT (CRUSTACEA: DECAPODA: RHYNCHOCINETIDAE)

JUNJI OKUNO

OKUNO, J. 1997. A new shrimp of the genus *Rhynchocinetes* from the Great Australian Bight (Crustacea: Decapoda: Rhynchocinetidae). *Records of the South Australian Museum* 30(1): 13–18.

A new shrimp of the family Rhynchocinetidae, *Rhynchocinetes enigma*, is described and illustrated on the basis of two males and an ovigerous female from the Great Australian Bight. This species is readily distinguished from the other eleven congeners by the absence of an arthrobranch from the third maxilliped, or lack of an arthrobranch on the pereopods. It represents the fourth rhynchocinetid species from depths exceeding 100 m.

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Caridean shrimps belonging to the family Rhynchocinetidae are distinguished from other carideans in the combination of having a typically movable rostrum, fine transverse striae on the surface of the carapace and abdominal somites, the first two pairs of pereopods robust, with fingers bearing long lateral and terminal spines, and the second pereopod with the carpus entire, not subdivided. To date, this family includes two genera, *Rhynchocinetes* H. Milne-Edwards and *Cinetorhynchus* Holthuis (Okuno 1996b, in press).

Through the courtesy of Ms K. Gowlett-Holmes of the South Australian Museum, Adelaide (SAM), I was able to examine two male and one ovigerous female specimens of an unfamiliar *Rhynchocinetes* species collected by trawling from the Great Australian Bight at depths between 113 and 170 m. These specimens do not possess arthrobranches, although the previously described congeners at least have arthrobranches on the third maxilliped and the first pereopod. Because of these differences, they are described herein as new species.

The postorbital carapace is abbreviated as CL, and the type specimens are deposited in SAM.

***Rhynchocinetes enigma* sp. nov.**
(Figs. 1–3)

Material Examined

Holotype. Male (SAM C5599, 6.8 mm CL), 34°17'S, 132°42'E, Great Australian Bight,

approximately 15 km west-south-west of Pearson Islands, 140–160 m depth, 'F. V. Comet', April 16, 1989.

Paratypes. Ovigerous female (SAM C5598, 9.0 mm CL), 33°12'S, 130°53'E, Great Australian Bight, 250 km south-south-west of Ceduna, 113 m depth, 'F. R. V. Soela', August 5, 1981. Male (SAM C5600, 7.6 mm CL), 33°18'S, 127°38'E, Great Australian Bight, approximately 115 km south-west of Eucla, 170 m depth, 'F. V. Comet', January 17, 1989.

Diagnosis

A species of *Rhynchocinetes* without arthrobranches on maxillipeds and pereopods. Dorsal rostral margin armed with three subterminal teeth. Fourth abdominal somite with distinct posteroventral tooth on pleuron. Ambulatory pereopods with meri bearing three spines, and dactyli with four accessory claws posterior to terminal claw. Endopod of male first pleopod with distinct lobe on outer margin.

Description

Carapace (Fig. 2A) covered with fine transverse striae, armed with two acute teeth on dorsal median carina, anterior tooth just behind rostral articulation, posterior tooth feebly articulated with carapace; supraorbital spine acute, considerably longer than spines on dorsal median carina, directed anteriorly; antennal spine acute, supported by a feeble carina, directed anteriorly; pterygostomial spine small, distinct. Rostrum (Fig. 2A) articulated with carapace, 1.10–1.28x as long as carapace; dorsal margin armed with

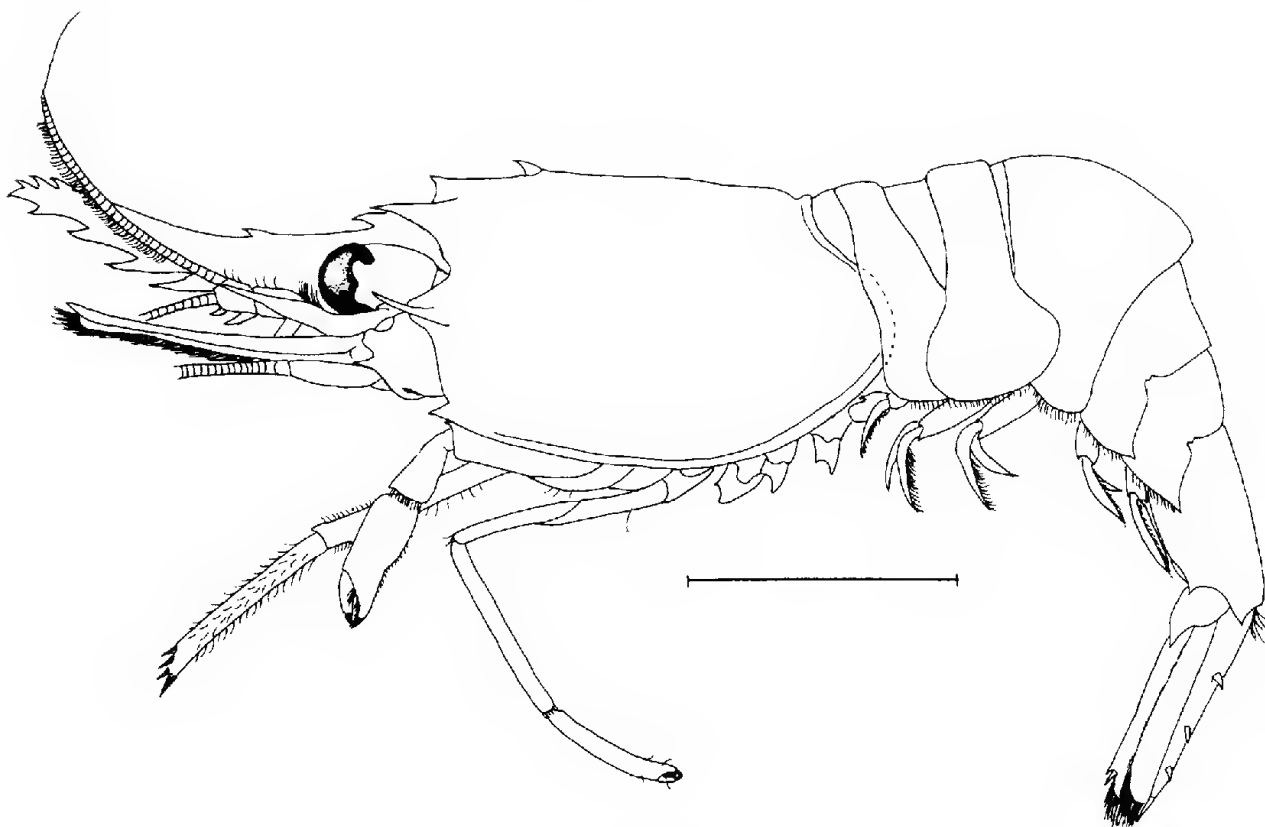


FIGURE 1. *Rhynchocinetes enigma* sp. nov., holotype male (SAM C5599, 6.8 mm CL). Scale bar = 5 mm.

two teeth in the basal half, and with three small teeth subterminally; ventral margin armed with eleven teeth, large proximally, elongate, decreasing distally.

Abdominal somites (Fig. 1) covered with fine striae; first three somites with the pleuron marginally rounded; pleura of fourth and fifth somites with distinct posteroventral tooth; sixth somite $0.48 - 0.50\times$ as long as carapace, with acute posteroventral spine, with strongly hooked anal spine between bases of uropods, directed posteriorly. Telson (Fig. 2B) $0.57 - 0.63\times$ as long as carapace, $1.16 - 1.30\times$ as long as sixth abdominal somite, armed dorsally with three pairs of spines; midpoint of posterior margin triangularly produced, with three pairs of spines, median pair longest.

Eyes well developed, with large, globular cornea; stalk much more slender than cornea.

Antennular peduncle (Fig. 2C) reaching midlength of scaphocerite; stylocerite long, reaching or slightly shorter than level of distal margin of antennular distal segment; proximal segment with distolateral spine reaching distal margin of antennular median segment and small proximal lateral tooth, ventrally with acute spine

at mesial margin; thickened part of upper antennular flagellum slightly overreaching rostral apex.

Antenna (Fig. 2D) with scaphocerite $0.84 - 0.93\times$ as long as carapace, $4.20\times$ as long as maximum width, distolateral spine acute, distinctly overreaching end of lamella; carpocerite reaching proximal quarter length of scaphocerite; basicerite with acute ventrolateral spine and with rounded protrusion just above the spine.

Mandible (Fig. 3A) with robust three-segmented palp, distal segment rounded, with dense setae marginally; incisor process well developed, with six marginal teeth; molar process obliquely truncate distally, with finely ridged distal end.

First maxilla (Fig. 3B) with slender palp armed distally with single long stout spiniform setae; proximal endite distinct, rounded, marginally with numerous setae; distal endite armed with ten stout spines on mesial margin.

Second maxilla (Fig. 3C) with well developed tapering palp; proximal endite slightly truncate; distal endite bilobed, upper lobe rather broader than lower lobe; scaphognathite large, overreaching level of tip of palp, anterior lobe with

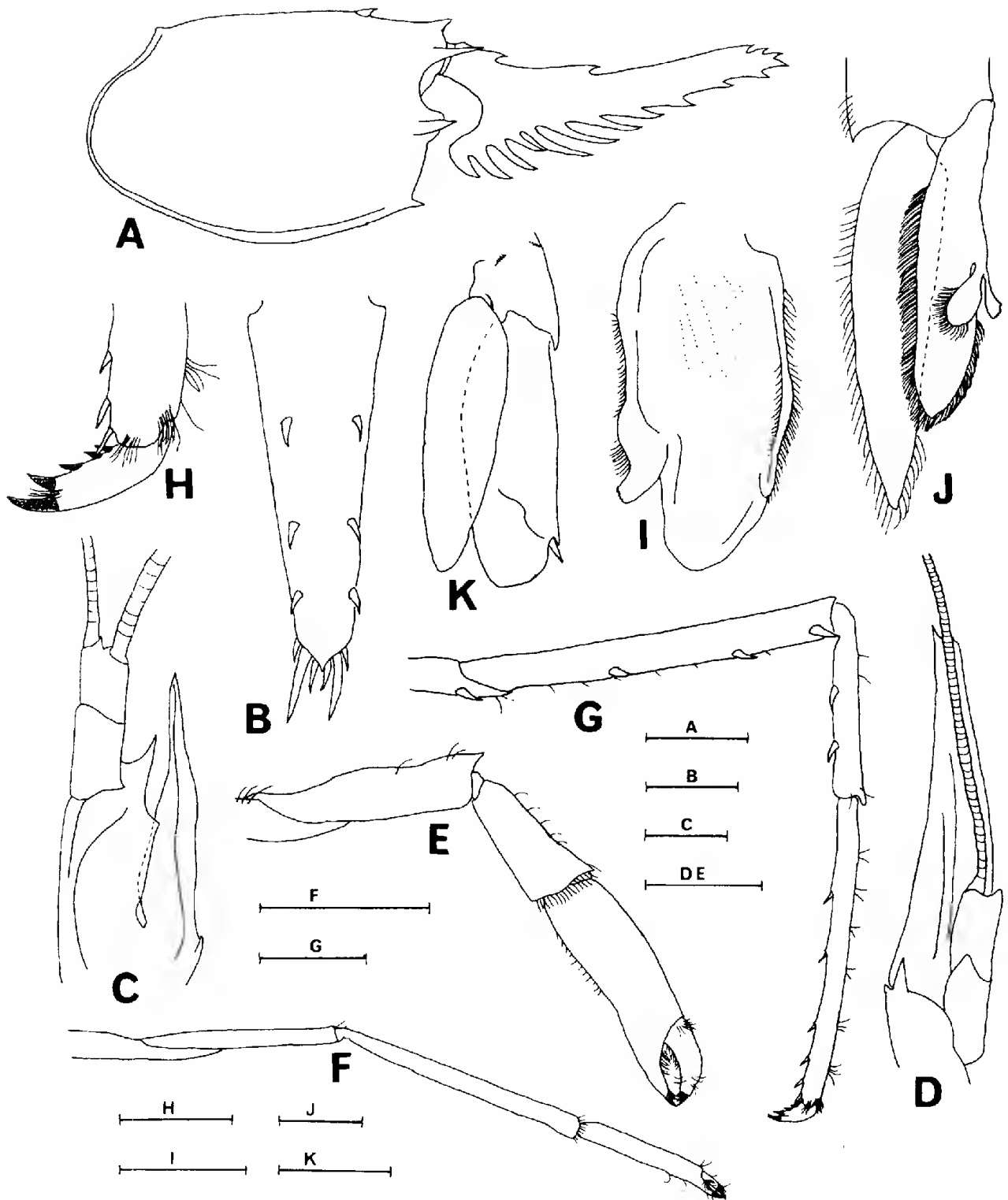


FIGURE 2. *Rhynchocinetes enigma* sp. nov., holotype male (SAM C5599, 6.8 mm CL). A, carapace with rostrum; B, telson, dorsal aspect; C, right antennular peduncle, dorsal aspect; D, right antenna, ventral aspect; E, right first pereiopod; F, right second pereiopod; G, right third pereiopod; H, same dactylus; I, endopod of right first pleopod; J, right second pleopod; K, right uropod, dorsal aspect. Scale bars; A = 2.5 mm; B, C = 1 mm; D, K = 2 mm; E, G = 1.5 mm; F = 3 mm; H-J = 0.5 mm.

TABLE 1. *Rhynchocinetes enigma*, new species. Branchial formula.

	Maxillipeds			Pereiopods				
	I	II	III	I	II	III	IV	V
Pleurobranchs	—	—	—	1	1	1	1	1
Arthrobranchs	—	—	—	—	—	—	—	—
Podobranchs	—	1	—	—	—	—	—	—
Epipods	1	I	I	1	1	1	1	—
Exopods	1	1	I	—	—	—	—	—

feebly quadrate distal end, posterior lobe tapering, with clongate plumose setae posteriorly, mesial margin convex.

First maxilliped (Fig. 3D) with endites distinctly separated, distal endite concave marginally, distinctly larger than proximal endite with slightly rounded margin; palp long, apparently two-segmented; exopod with long flagellum, caridean lobe distinct.

Second maxilliped (Fig. 3E) with well developed podobranch; epipod slightly pointed distally; exopod well developed, tapering; dactylar segment with truncate distal margin; propodal segment with external margin rounded, mesial margin expanded; ischiomeral segment distinct.

Third maxilliped (Fig. 3F) slightly shorter than tip of scaphocerite; exopod slightly shorter than distal margin of antepenultimate segment, tapering, with dense long setae; ultimate segment with six spines terminally, 0.59 – 0.62x as long as carapace, 2.00 – 2.24x as long as penultimate segment; penultimate segment 0.28 – 0.29x as long as carapace.

Branchial formula as shown in Table 1.

First pereiopod (Fig. 2E) chelate, moderately robust, falling slightly short of midlength of scaphocerite; chela 0.44 – 0.45x as long as carapace, 2.00 – 2.24x as long as carpus, tips of both fingers with dark terminal claws; carpus 0.21 – 0.25x as long as carapace, with acute spine at distal end of dorsal margin; merus dorsodistally acute.

Second pereiopod (Fig. 2F) chelate, much more slender than first pereiopod, reaching distal sixth of length of scaphocerite; chela 0.40x as long as carapace; carpus entire, 0.59 – 0.65x as long as carapace, 1.50 – 2.03x as long as chela.

Third pereiopod (Fig. 2G) reaching distal end of scaphocerite; ischium with single spine; merus 0.74 – 0.81x as long as carapace, 1.50 – 2.03x as long as carpus, with three almost equidistant spines; carpus 0.37 – 0.41x as long as carapace,

with two spines on outer surface; propodus 0.69x as long as carapace, 1.68x as long as carpus, with about six short spinules on flexor margin; dactylus (Fig. 2H) with four accessory claws posterior to terminal largest claw, decreasing in size proximally.

Fourth pereiopod reaching distal fifth of length of scaphocerite, spinulation resembling that of third pereiopod; merus 0.67 – 0.72x as long as carapace, 1.86 – 1.94x as long as carpus; carpus 0.34 – 0.38x as long as carapace; propodus 0.69x as long as carapace, 1.81x as long as carpus.

Fifth pereiopod slightly shorter than midlength of scaphocerite; spinulation resembling those of two anterior ambulatory pereiopods; merus 0.56 – 0.62x as long as carapace, 1.57 – 1.72x as long as carpus; carpus 0.32 – 0.37x as long as carapace; propodus 0.58 – 0.66x as long as carapace, 1.79 – 1.80x as long as carpus.

Endopod of male first pleopod (Fig. 2I) with distal end rounded; well developed appendix interna at midlength of mesial margin, distal end of appendix with dense cincinnuli; distinct lobe at distal third of outer margin of endopod.

Endopod of male second pleopod (Fig. 2J) with appendices masculina and interna at distal two fifths of outer margin; appendix masculina broad, with distal margin rounded, fringed with dense setae; appendix interna considerably more slender and shorter than appendix masculina, with dense cincinnuli at distal end.

Uropodal exopod and endopod (Fig. 2K) slightly overreaching distal end of telson, exopod with a fixed and a movable spine at distal fifth of outer margin, the former considerably shorter than the latter.

Coloration

Unknown.

Distribution

Known only from the Great Australian Bight.

DISCUSSION

Most rhynchocinetid shrimps are found around coral or rocky reefs in shallow waters, although three species, *R. australis* Hale, 1941, *R. balssi* Gordon, 1936 and *R. ikatere* Yaldwyn, 1971 are known from deep waters at depths in excess of 100 m (Hale 1941, Yaldwyn 1971, Holthuis 1972). The present new species represents the fourth rhynchocinetid shrimp obtained from such deep waters. Okuno (1996a) suggested that the

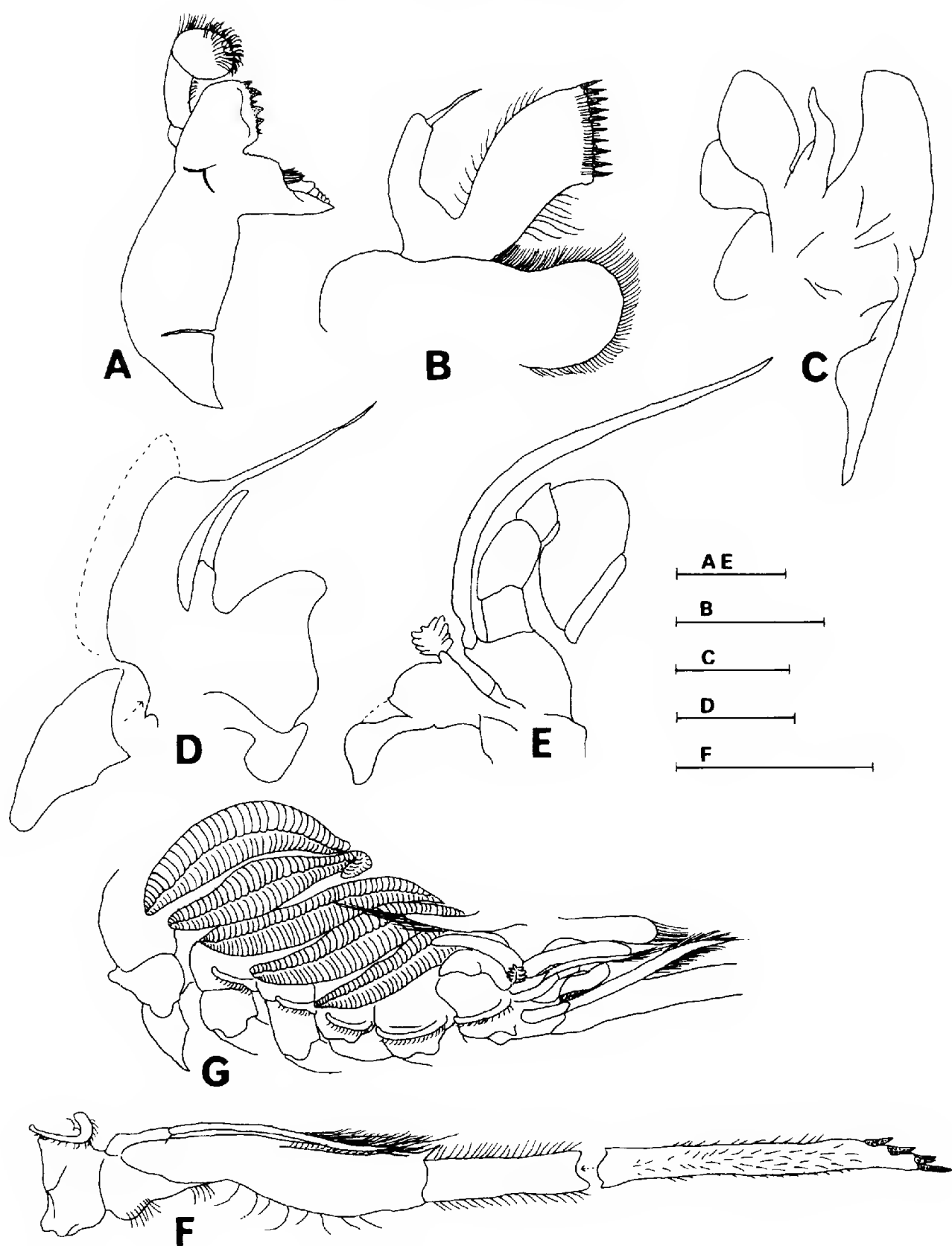


FIGURE 3. *Rhynchocinetes enigma* sp. nov., paratype male (SAM C5600, 7.6 mm CL). **A**, right mandible; **B**, right first maxilla; **C**, right second maxilla; **D**, right first maxilliped; **E**, right second maxilliped; **F**, right third maxilliped; **G**, right branchial region. Setae omitted on C, D, E. Scale bars; A–E = 1 mm; F = 2 mm; G = 3 mm.

TABLE 2. Specific list of *Rhynchocinetes* accompanied with number of arthrobranch (max. = maxilliped; per. = pereopod).

	3rd max.	1st per.	2nd per.	3rd per.	4th per.	5th per.
<i>R. australis</i> Halc	2	1	1	—	—	—
<i>R. balssi</i> Gordon	2	1	—	—	—	—
<i>R. brucei</i> Okuno	2	1	1	1	—	—
<i>R. conspiciocellus</i> Okuno et Takada	2	1	1	—	—	—
<i>R. durbanensis</i> Gordon	2	1	1	1	—	—
<i>R. enigma</i> sp. nov.	—	—	—	—	—	—
<i>R. ikatere</i> Yaldwyn	2	1	1	—	—	—
<i>R. kuiteri</i> Tiefenbacher	2	1	1	1	—	—
<i>R. rathbunae</i> Okuno	2	1	1	1	—	—
<i>R. serratus</i> (H. Milne-Edwards)	2	1	1	1	—	—
<i>R. typus</i> H. Milne-Edwards	2	1	1	1	1	—
<i>R. uritai</i> Kubo	2	1	1	—	—	—

temperate and subtropical *Rhynchocinetes* species all have a limited distributional range. Therefore, *R. enigma* probably occurs in southern Australian waters only.

Eleven species belonging to the genus *Rhynchocinetes* were previously known (Okuno 1996a). *Rhynchocinetes enigma* differs distinctly from the other species by the absence of an arthrobranch on all the maxillipeds and pereopods (Fig. 3G). The other *Rhynchocinetes* species always have two small arthrobranches on the third maxilliped and a developed arthrobranch on at least the first pereopod (Table 2). In both *Rhynchocinetes* and *Cinetorhynchus*, the number of arthrobranches varies at the species level (see Table 2; Okuno 1996b), and except for the number of arthrobranches, there is no unique morphological

character that distinguishes the new species from other *Rhynchocinetes* species. Therefore, I am inclined to place the new species in *Rhynchocinetes*, rather than establishing a new genus to accommodate it.

Etymology

The species name *enigma* refers to the enigmatical status within the genus, because of the absence of all arthrobranches.

ACKNOWLEDGMENTS

I am grateful to Ms K. Gowlett-Holmes for sending me the specimens on loan. I also thank Dr L. B. Holthuis for critically reading the manuscript and giving me valuable suggestions.

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**POMPHORHYNCHUS HERONENSIS SP. NOV. (ACANTHOCEPHALA:
POMPHORHYNCHIDAE) FROM LUTJANUS CARPNOTATUS
(LUTJANIDAE) FROM HERON ISLAND, AUSTRALIA**

SYLVIE PICHELIN

Summary

Pomphorhynchus heronensis sp. nov. is described from *Lutjanus carponotatus* (lutjanidae) from Heron Island, Australia. The new species can be distinguished easily from all other species of the genus by the combination of the following characters: a relatively short neck with a symmetrical bulb (bulb/total neck length ratio = 1: 0.5), 15-17 longitudinal rows with 13-16 hooks per row of which the apical hooks (7-8 per row) have roots and are larger than the basal hooks and are arranged in slightly spiral rows whereas the basal hooks (6-8 per row) have no roots and are arranged in straight rows, a proboscis receptacle that does not extend beyond the bulb and atypical cement glands. This is the first species of *Pomphorhynchus* described from Australia and represents one of the few species of that genus known from a marine host.

**POMPHORHYNCHUS HERONENSIS SP. NOV. (ACANTHOCEPHALA:
POMPHORHYNCHIDAE) FROM *LUTJANUS CARPONOTATUS* (LUTJANIDAE)
FROM HERON ISLAND, AUSTRALIA**

SYLVIE PICHELIN

PICHELIN, S. 1997. *Pomphorhynchus heronensis* sp. nov. (Acanthocephala: Pomphorhynchidae) from *Lutjanus carponotatus* (Lutjanidae) from Heron Island, Australia. *Records of the South Australian Museum* 30(1): 19–27.

Pomphorhynchus heronensis sp. nov. is described from *Lutjanus carponotatus* (Lutjanidae) from Heron Island, Australia. The new species can be distinguished easily from all other species of the genus by the combination of the following characters: a relatively short neck with a symmetrical bulb (bulb/total neck length ratio = 1: 0.5), 15–17 longitudinal rows with 13–16 hooks per row of which the apical hooks (7–8 per row) have roots and are larger than the basal hooks and are arranged in slightly spiral rows whereas the basal hooks (6–8 per row) have no roots and are arranged in straight rows, a proboscis receptacle that does not extend beyond the bulb and atypical cement glands. This is the first species of *Pomphorhynchus* described from Australia and represents one of the few species of that genus known from a marine host.

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Manuscript received 29 April 1996.

There are four genera of Pomphorhynchidae: *Pomphorhynchus* Monticelli, 1905, *Longicollum* Yamaguti, 1935, *Tenuiproboscis* Yamaguti, 1935 and *Paralongicollum* Amin, Bauer and Sidorov, 1991. Of these, only species of *Longicollum* have been recorded in Australia (Edmonds 1989, Roubal 1993). There are about 25 species of *Pomphorhynchus* (see Amin 1985, Ortubay *et al.* 1991, Wang & Guo 1983). This study describes a new species of *Pomphorhynchus* from *Lutjanus carponotatus* (Lutjanidae) from Heron Island, Australia.

MATERIALS AND METHODS

Twelve *Lutjanus carponotatus* were collected using handlines in the Wistari Channel, Heron Island and dissected for parasites. Acanthocephalans were removed from the intestine; host tissue surrounding the neck including the bulb of the worms was removed using micropins and forceps. Specimens were placed in a cavity block in tap water and refrigerated to encourage the eversion of the proboscis and then fixed in Berland's fluid and stored in 70% alcohol. Specimens were stained with Mayer's haematoxylin and mounted in Canada balsam. Lactophenol was used to clear specimens temporarily for description and measurement. Some worms were critical point

dried, gold sputter-coated and examined under a scanning electron microscope operating at 5–10 kV. Some worms were serially sectioned and stained with Mayer's haematoxylin and eosin. Drawings were made with the aid of a *camera lucida* and added to by hand. Measurements, presented as the range with the mean followed by the standard deviation in parenthesis, are given in micrometres; where measurements are presented in paired sets separated by a multiplication sign, the first figure is length, the second width. Sample size is given after each measurement. Type material has been deposited in the Australian Helminthological Collection (AHC), South Australian Museum.

SYSTEMATICS

Class PALAEACANTHOCEPHALA

Family POMPHORHYNCHIDAE Yamaguti, 1939

Genus *Pomphorhynchus* Monticelli, 1905

Pomphorhynchus heronensis sp. nov.
(Figs 1–7)

Type host: *Lutjanus carponotatus* (Lutjanidae).

Other hosts: two specimens from intestine of 1 of

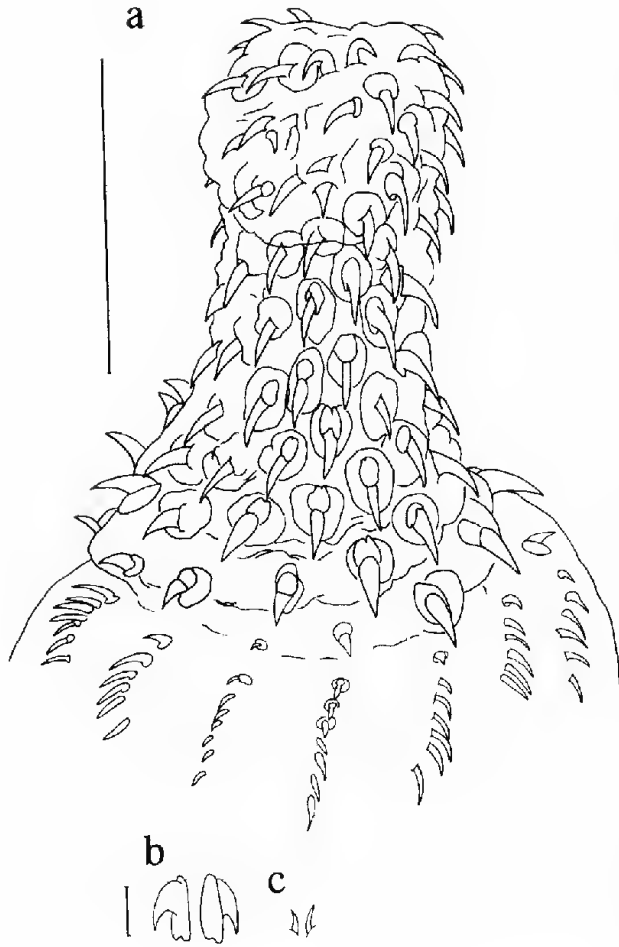


FIGURE 1. **a**, Proboscis showing two distinct hook types, **b**, apical hooks, and **c**, basal hooks on proboscis. Scale bars: **a** = 200, **b** and **c** = 20.

5 *Cheilinus trilobatus* (Labridae) from Heron I., Qld, Aust.

Type site: Rectum – neck and proboscis of parasites bulging through rectal wall into body cavity of host; infections easily diagnosed from outside gut.

Type locality: Heron I. (23°27' S, 151°55' E), Qld, Aust.

Material: holotype (male) AHC 30345; paratypes AHC 27665–27683, 30346.

Infection rate: 9 of 12 infected.

Description

General

Proboscis cone to pear shaped with slight anterior swelling; 2 distinct types of hooks (Figs 1a–c, 2) present. Apical proboscis hooks large 29.5–51.0 ($43.2 \pm \text{s.d. } 6.6$) ($n=19$) (Fig. 1b); root 25.3–48.5 ($39.6 \pm \text{s.d. } 4.7$) ($n=15$) with slight indentation of base; hooks arranged in 15–17

slightly spiralling rows of 7–8 hooks per row. Basal proboscis hooks small 14.8–23.5 ($18.2 \pm \text{s.d. } 2.3$) ($n=10$) (Fig. 1c), slender with vestigial or no roots arranged in 15–17 straight rows of 6–8 hooks per row. Neck short (neck length: trunk length = 1: 0.32–0.61 (1: 0.44 $\pm$ s.d. 0.09) ($n=20$)), uniformly cylindrical from trunk level until abruptly swells to form symmetrical bulb encircling neck; bulb without protrusions or other irregularities, may be either spherical or slightly wider than long. Proboscis receptacle 923–1307 ($1100 \pm \text{s.d. } 123$) $\times$ 161–231 ($188 \pm \text{s.d. } 23$) ($n=10$) (Fig. 3) double walled, extends from base of proboscis to base of bulb; does not extend into trunk. Trunk widest anteriorly, tapering posteriorly. Lemnisci 2, slender, 980–2674 ($1696 \pm \text{s.d. } 702$) ($n=6$) long.

Males

Total length 7780–13500 ($10724 \pm \text{s.d. } 2213$) ($n=15$) (Fig. 4). Trunk 5520–10000 ($7409 \pm \text{s.d. } 1426$) $\times$ 1000–2120 ($1572 \pm \text{s.d. } 357$) ($n=11$) at widest point. Neck length including bulb 2250–3440 ($2735 \pm \text{s.d. } 522$) ($n=6$); neck width excluding bulb 280–620 ($392 \pm \text{s.d. } 100$) ($n=10$); bulb 950–1900 ($1362 \pm \text{s.d. } 369$) ($n=6$) $\times$ 1360–2500 ($1856 \pm \text{s.d. } 441$) ($n=5$); bulb/total neck length ratio 1: 0.42–0.59 (1: 0.5) ($n=6$). Lemnisci do not extend beyond anteriormost testis. Testes 2, ovoid, 360–840 ($609 \pm \text{s.d. } 124$) $\times$ 246–520 ($377 \pm \text{s.d. } 90$) ($n=14$), in tandem or diagonal, in anterior third of trunk. Cement glands number undetermined, probably 2 (Figs 5a–c); glands pyriform at level of seminal vesicle but become tubular and convoluted as they extend to posteriormost margin of testis. Proximal part of cement glands, seminal vesicle and Säftigen's pouch contained within genital sheath (Fig. 5a); ligament sac envelops convoluted tubular part of cement glands, sperm duct and testes. Säftigen's pouch pyriform, widest part measures 538 ($n=1$), thick-walled, partly enveloped by cement glands. Sperm duct emerges from seminal vesicle, runs anteriorly to testes; union of sperm duct and testes not seen. Seminal vesicle small, obscured by proximal part of cement glands. Bursa with pointed digitiform rays and 2 concentric rings of circumbursal receptors (Fig. 6).

Females

Total length 6630–14000 ($9593 \pm \text{s.d. } 2317$) ($n=21$) (Fig. 7a). Trunk 4300–8540 ($6157 \pm \text{s.d. } 1194$) $\times$ 1200–2960 ($1761 \pm \text{s.d. } 310$) ($n=16$) at widest point. Neck length including bulb, 2000–3700 ($2703 \pm \text{s.d. } 445$) ($n=14$); neck width



FIGURE 2. SEM of proboscis showing apical hook (arrow) and basal hook (arrowhead). Scale bar = 50.

excluding bulb 300–500 ($373 \pm \text{s.d. } 42$) ($n=14$); bulb 900–1900 ($1333 \pm \text{s.d. } 350$) $\times$ 1250–2400 ($1699 \pm \text{s.d. } 444$) ($n=16$); bulb/total neck length 1: 0.41–0.59 (1: 0.50) ($n=14$). Female reproductive system consists of ovarian balls, ligament sac, uterine bell, uterus, well formed vaginal funnel, 2 consecutive vaginal sphincters and bulb (Fig. 7b); ligament sac broken in all specimens examined. Eggs ovoid to fusiform with small polar prolongations of middle membrane (Fig. 7c), 98–129 ($112 \pm \text{s.d. } 7$) $\times$ 27–35 ($33 \pm \text{s.d. } 3$) ($n=15$); eggs may be present in neck and bulb.

DISCUSSION

The present specimens belong to the genus *Pomphorhynchus* according to acanthocephalan keys by Amin (1987a) and Amin *et al.* (1991) because they have a neck with a true bulb anteriorly and lack the spirally twisted neck which is characteristic of *Longicollum*.

The number of rows of hooks and the number of hooks per row are similar in most species of *Pomphorhynchus* including *Pomphorhynchus heroenensis* sp. nov. However, all species of *Pomphorhynchus* except *P. heroenensis* appear to

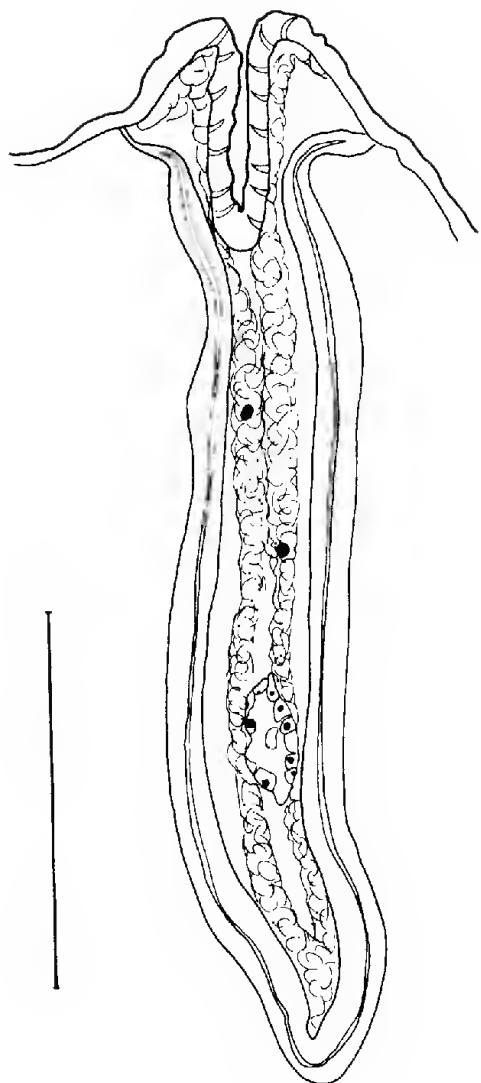


FIGURE 3. Horizontal section through the proboscis receptacle. Scale bar = 500.

have a proboscis receptacle that extends well beyond the bulb and, in many instances, into the trunk. The atypical shape and number of the cement glands in *P. heronensis* (see below) also distinguishes it from all other pomphorhynchid species. Further features that can differentiate this new species from other similar species of *Pomphorhynchus* are given below. The new species can further be differentiated from *P. patagonicus* Ortubay, Ubeda, Semenas and Kennedy, 1991, *P. sebastichthydis* Yamaguti, 1939 and *P. yamagutii* Schmidt and Huggins, 1973 because they possess asymmetrical bulbs (Ortubay *et al.* 1991, Schmidt & Huggins 1973, Yamaguti 1939). *Pomphorhynchus yunanensis* Wang, 1981 differs by having 12 rows of hooks with only 5-6 proboscis hooks per row (Wang

1981). *P. lucyi* Williams and Rogers, 1984 differs by having a considerably longer neck (Williams & Rogers 1984) relative to that of *P. heronensis*. *Pomphorhynchus cylindricus* Wang and Guo, 1983 and *P. bosniacus* Kiskároly and Čanković, 1969 have fewer than 15 rows of proboscis hooks with 9 or fewer hooks per row (Wang and Guo 1983, Kiskároly & Čanković 1969); also the testes of *P. cylindricus* are more posterior than those of *P. heronensis*. *Pomphorhynchus laevis* (Zoege in Müller, 1776) and *P. intermedius* Engelbrecht, 1957 have the last basal hooks on the proboscis

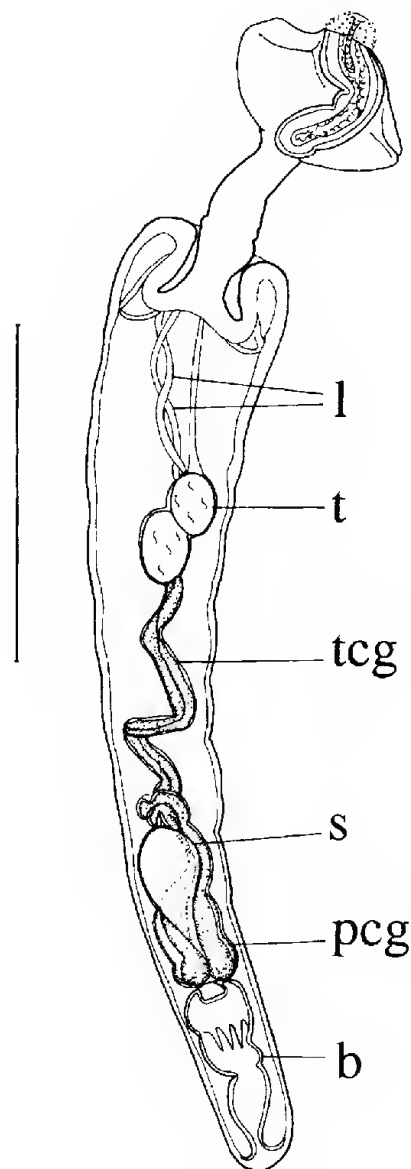


FIGURE 4. Male specimen (holotype), bulb slightly collapsed. Scale bar = 2000. Legend: l, lemnisci; t, testis; tcg, tubular part of cement glands; s, Säffigen's pouch; pcg, posterior part of cement glands; b, bursa with bursal rays.

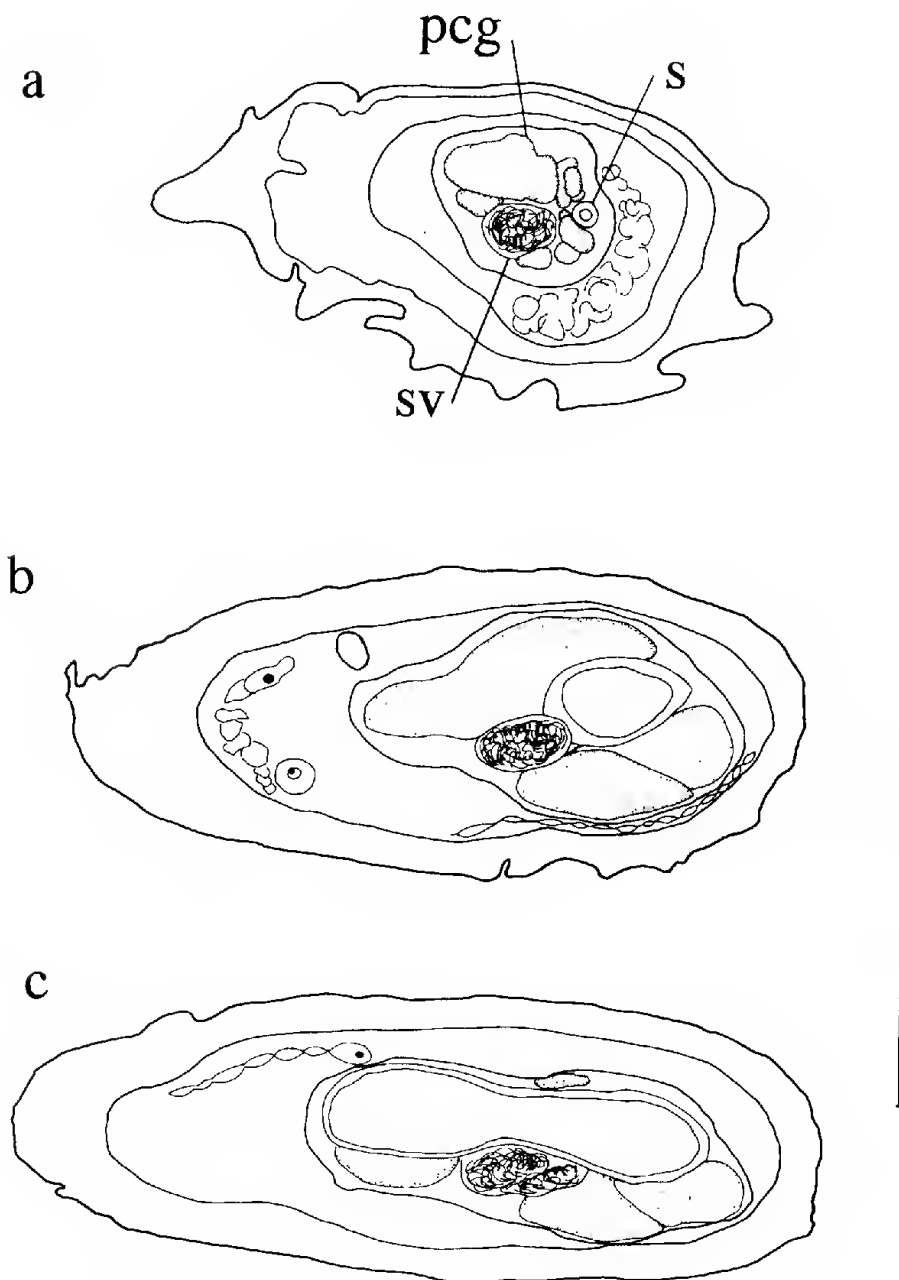


FIGURE 5. Transverse sections through a male specimen showing: **a**, the proximal ends of Säfteggen's pouch, cement glands and seminal vesicle; **b**, the cement glands partially enveloping Säfteggen's pouch (160 μ further anterior from previous section); **c**, the widening of Säfteggen's pouch (70 μ from previous section). Fig. 5a–c drawn to same scale. Scale bar = 500. Legend: s, Säfteggen's pouch; pcg, posterior part of cement glands; sv, seminal vesicle.

larger than those immediately preceding (Golvan 1969). *P. heronensis* does not have this feature; the last basal hook only appears longer when the other hooks of *P. heronensis* are not fully exposed. *P. intermedius*, like many other species of the genus, does not appear to possess the two very distinct sizes of hooks on the proboscis seen in the new species. Two distinct sizes of hooks can be seen on the proboscis of *P. laevis* as shown in

Brown *et al.* (1986, Fig. 5) but in addition to the differences mentioned above *P. laevis* has fewer hooks per row (13–20 rows with 8–13 hooks) (Brown *et al.* 1986) than *P. heronensis*. Thus, the new species can be distinguished easily from all other species of the genus by the combination of the following characters: a relatively short neck with a symmetrical bulb (bulb/total neck length ratio 1:0.5; neck including bulb/trunk length ratio

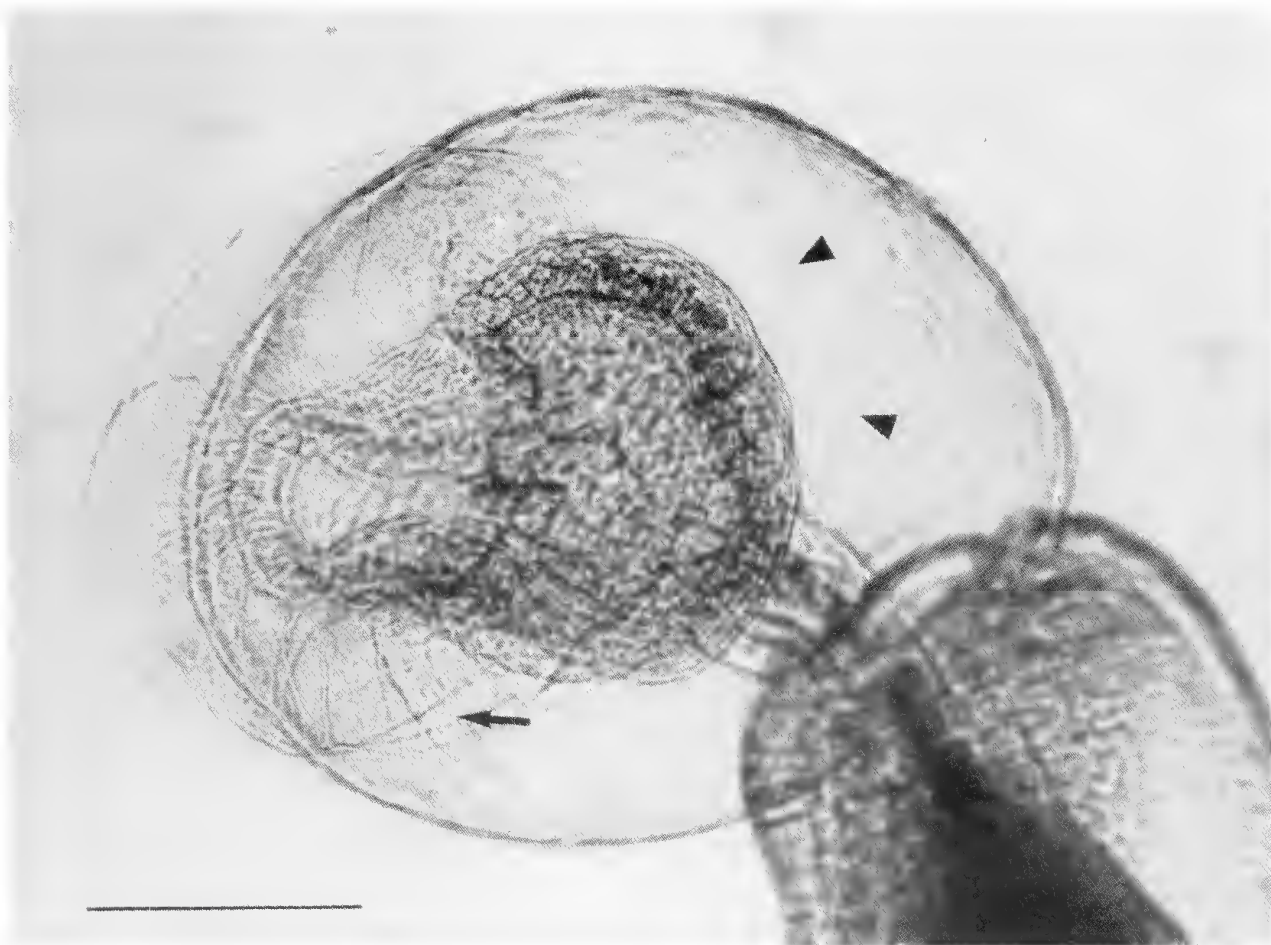


FIGURE 6. Light photomicrograph of cloacal bursa showing bursal rays (arrow) and two circles of circumbursal receptors (arrowheads). Scale bar = 250.

1:0.44), 15–17 longitudinal rows with 13–16 hooks per row of which the apical hooks (7–8 per row) have roots and are larger than the basal hooks and are arranged in slightly spiral rows whereas the basal hooks (6–8 per row) have no roots and are arranged in straight rows, a proboscis receptacle that does not extend beyond the bulb and atypical cement glands.

Some females, but not males, of the new species show deformities similar to those described by Amin *et al.* (1991) for specimens of *Paralongicollum nemacheili* Amin *et al.*, 1991. Other than the enlarged dorsal trunk region, deformed females did not appear to differ from normal females. Both normal and deformed females had eggs that were dispersed throughout the trunk and occasionally into the bulb; no eggs were present in the deformed part of the gravid female. The presence of eggs in the bulb seems uncommon in other pomphorhynchids but has been reported in *P. kashmirensis* Kaw, 1941 by

Kaw (1941) and in *P. sebastichthydis* by Yamaguti (1939). The presence of eggs may well be an artefact of the method of fixing or preserving and is certainly not a useful taxonomic character.

The cement glands of *P. heronensis* appear atypical for the family. Normally, pomphorhynchids are said to have six cement glands. In this species however, there appear to be only two very long glands. A study of serial sections showed that the proximal part of the glands are pyriform and closely surround Säftigen's pouch and the seminal vesicle. The glands then narrow out and run alongside the sperm duct up to the testes. Monorchic specimens of *P. heronensis* ($n=2$) appear to have the same arrangement of cement glands as normal males. Cement glands in species of *Pomphorhynchus* are not usually long but there is at least one other species, *Filisoma longcementglandatus* Amin and Nahhas, 1994, that has cement glands that may reach up to 16.00 mm in length (Amin & Nahhas,

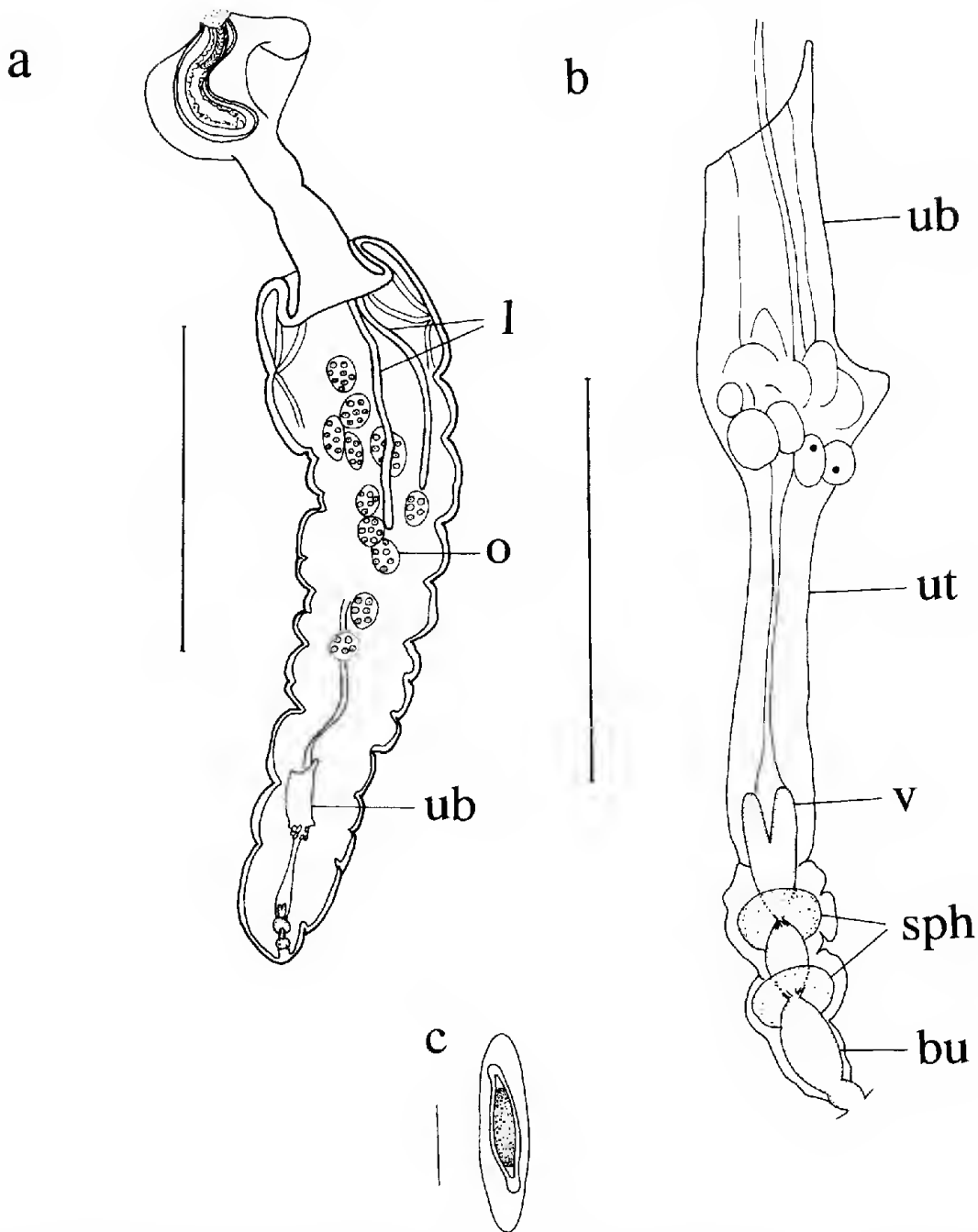


FIGURE 7. **a**, Female specimen, bulb slightly collapsed, **b**, uterine bell, **c**, egg. Scale bars: **a**=2000, **b**=500, **c**=50. Legend: **l**, lemnisci; **o**, ovarian ball; **ub**, uterine bell; **ut**, uterus; **v**, vaginal funnel; **sph**, sphincters, **bu**, bulb.

1994). Why *P. heronensis* should have cement glands so different from other pomphorhynchids is unknown. It is proposed here that the generic diagnosis be amended to include the variable nature of the cement glands seen in *P. heronensis*.

Two circles of circumbursal receptors similar to those described by Brown (1987) were seen in one male specimen. Bursal rays were also noted in the same specimen. Neither circumpenial receptors nor muscular suckers in the bursa as those

described by Brown (1987) and Doyle and Gleason (1991) could be seen in the new species. Although Brown (1987) considered the receptors may be useful taxonomically, these structures were not used as such in this paper because they were difficult to see. Brown (1987, Fig. 3) also showed the presence of vesicles in the bursa. However, Doyle and Gleason (1991) reported muscular suckers on the inner bursal surface and suggested that the vesicles noted by Brown (1987)

could have been a ballooning out of the muscular suckers caused by the method of preparation. A male with an hyperextended bursa would probably not be able to hold the female in position and thus fail to copulate.

Many acanthocephalans show size dimorphism; noteworthy is that both males and females of *P. heronensis* appear to be the same length. Also, there appeared to be an absence of very young stages. Although some juvenile pomphorhynchids appear able to detach from the gut, move and reattach to another region (Amin 1987b) no pomphorhynchids in the present study were found other than in the rectum. The lack of juvenile stages may indicate that hosts are not continuously infected throughout the year or that there is some mechanism restricting establishment of new parasites. Brown (1986) provided evidence to show that populations of *P. laevis* could reach a ceiling level and that parasite establishment could be density-dependent. However, in some cases it appears that this ceiling level is not reached because the critical resource, e.g. space, is only limited briefly (Bates & Kennedy 1991).

Pomphorhynchids have been recorded from a wide range of teleosts (see Golvan & de Buron 1988). Amin (1987c) recognised three categories of hosts for *P. bulbocolli* Linkins in Van Cleave, 1919: principal, accessory and occasional hosts. In this study, *L. carponotatus* is considered as a principal host for *P. heronensis* because female pomphorhynchids with ovarian balls, immature and mature shelled acanthors were regularly recovered, all parasites were firmly attached and none were found extraintestinally. This is consistent with the findings by Brown *et al.* (1986) and Amin (1987c) who considered the regular presence of mature gravid females as an indication that the parasite is in its preferred definitive host. It is also consistent with the observations made by Kennedy (1984) that *P. laevis* in its non-preferred hosts were smaller, immature, weakly attached and many were recovered in extraintestinal sites.

Most species of *Pomphorhynchus* occur in

freshwater fishes. Some exceptions such as *Pomphorhynchus laevis* have been recorded from both freshwater and marine fishes (see, for example, Kennedy 1984). Although, it has been suggested that the freshwater *P. laevis* is a different strain from the marine *P. laevis* and that each strain has a preferred host (see Kennedy 1984); currently there is thought to be three strains (see Kennedy *et al.* 1989, Kennedy 1996). The preferred position in the preferred marine host of *P. laevis* is the rectum whereas the preferred position in freshwater host is more anterior (see Kennedy 1984). All the specimens of *P. heronensis* recovered for this study were found in the rectum of its host, *L. carponotatus*. *Lutjanus carponotatus* is not known from freshwater habitats (Allen & Talbot 1985) and thus the posterior position of the parasite cannot be correlated with a response to changing salinity as shown by Kennedy (1984) for *P. laevis* under certain circumstances.

Specimens of *Pomphorhynchus heronensis* were also recovered from one of five *Cheilinus trilobatus* in the present study and from one of five from another study of helminths in fishes of Heron Island (Cribb *pers. comm.*). In these specimens the parts of the worms that had penetrated the gut wall (i.e. the neck including the bulb) were decayed. Had this deterioration resulted from the worms being reproductively exhausted followed by death *in situ*, then worms in similar condition should have been found in *L. carponotatus*; none were. It may be that *C. trilobatus* is an unsuitable or at best an occasional host for *P. heronensis* but further material is needed to negate the possibility of other factors influencing the presence or absence of these parasites, such as the distribution of intermediate hosts and seasonality.

ACKNOWLEDGMENTS

I am grateful to Dr T. H. Cribb for donating specimens of this species and reading this manuscript.

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FIELD IDENTIFICATION OF FEMALE LITTLE BROWN BATS VESPADELUS SPP. (CHIROPTERA : VESPERTILIONIDAE) IN SOUTH AUSTRALIA

L. F. QUEALE

Summary

Five morphologically similar species of little brown bats occur in South Australia; *Vespadelus finlaysoni*, *V. darlingtoni*, *V. regulus*, *V. baverstocki* and *V. vulturnus*. As males can be identified by the shape of their penes, the emphasis of this paper is on methods to differentiate the females of these similar species. Characters are listed here for identifying female *Vespadelus* bats, particularly for use in the field, using external measurements and geographic distribution data. *Vespadelus finlaysoni* and *V. darlingtoni* were found to be generally distinguished on size alone and *V. vulturnus* to be distinguished on a wing measurement ratio. *Vespadelus regulus* and *V. baverstocki* presented the greatest difficulty for identification. However this study shows that these two species can be distinguished 90% of the time. Areas of allopatry, parapatry and sympatry are also discussed.

FIELD IDENTIFICATION OF FEMALE LITTLE BROWN BATS *VESPADELUS* SPP. (CHIROPTERA : VESPERTILIONIDAE) IN SOUTH AUSTRALIA

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QUEALE, L. F. 1997. Field Identification of female little brown bats *Vespadelus* spp. (Chiroptera: Vespertilionidae) in South Australia. *Records of the South Australian Museum* 30(1): 29–33.

Five morphologically similar species of little brown bats occur in South Australia; *Vespadelus finlaysoni*, *V. darlingtoni*, *V. regulus*, *V. baverstocki* and *V. vulturnus*. As males can be identified by the shape of their penes, the emphasis of this paper is on methods to differentiate the females of these similar species. Characters are listed here for identifying female *Vespadelus* bats, particularly for use in the field, using external measurements and geographic distribution data. *Vespadelus finlaysoni* and *V. darlingtoni* were found to be generally distinguished on size alone and *V. vulturnus* to be distinguished on a wing measurement ratio. *Vespadelus regulus* and *V. baverstocki* presented the greatest difficulty for identification. However this study shows that these two species can be distinguished 90% of the time. Areas of allopatry, parapatry and sympatry of species are also discussed.

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Manuscript received 20 June 1996.

The bats once referred to as a single species of *Eptesicus* (*E. pumilus*) are now regarded as nine species of *Vespadelus* (Kitchener *et al.* 1987, Volleth & Tidemann 1991). This diversity has only recently been recognised and many of the species' morphologies are very similar, so that practical problems in the field of specimen identification have not yet been completely solved.

The current taxonomy follows Kitchener *et al.* (1987) who revised the genus using a combination of morphological features. Their conclusions were confirmed by allozyme electrophoresis (Adams *et al.* 1987) which showed a minimum of nine species. Males of the five South Australian species, *Vespadelus finlaysoni*, *V. darlingtoni*, *V. regulus*, *V. baverstocki* and *V. vulturnus*, can be unambiguously identified using penis glans morphology (Reardon & Flavel 1987) but a reliable method is not available for female morphology. Many of the characters used by Kitchener *et al.* (1987) were internal features and cannot be used for field identification. Geographic variation within species further complicates identification.

The aim of the present study was to provide simple field methods for identifying female *Vespadelus* spp. using external characters. Outside South Australia other workers have found that there is more overlap in forearm lengths between species (Tidemann 1981, Lumsden & Bennett 1995). I found that limiting this study to

South Australia, the task of identification can be made easier. These methods will prove useful in other states, although because of geographical variation there may be some differences.

MATERIALS AND METHODS

Initially, 127 adult female *Vespadelus* bats (9 *V. darlingtoni*, 11 *V. finlaysoni*, 50 *V. regulus*, 38 *V. baverstocki* and 15 *V. vulturnus*) from the spirit preserved mammal collection of the South Australian Museum were examined for this study. Adults were distinguished by ossification of wing bone epiphyses. Specimens in the collection were collected from widely separated localities to take account of regional variation within South Australia. Based on the results of previous investigations (Carpenter *et al.* 1978, McKean *et al.* 1978, Tidemann *et al.* 1981, Kitchener *et al.* 1987) and the ease of measurement and assessment, the following characters were selected for examination:

- 1) forearm (= radius) length
- 2) ratio of phalanx I to metacarpal length on digit III
- 3) geographic distribution
- 4) colour of skin and fur

Wing bone length measurements (to the nearest 0.1 mm) were taken, using dial calipers, from joint to joint (outside) when the joints were bent (see Reardon and Flavel 1987).

Distribution maps were compiled for each species using females that had been reliably identified by electrophoresis ($n=45$) and males identified by glans penes ($n=133$), following the method of Reardon and Flavel (1987).

General colour of skin and fur were also noted to aid identification.

To test the reliability of the characters described above, an additional 40 bats were analysed using electrophoresis of liver enzymes. The discriminating enzymes used were: aspartate aminotransferase, carbonate dehydratase, p-hosphogluconate dhydrogenase, dipeptidase, tripeptide aminopeptidase, glucose-6-phosphate isomerase, mannose-6-phosphate isomerase (see Adams *et al.* 1987).

RESULTS AND DISCUSSION

Forearm Length

Forearm ranges of *Vespadelus* spp. from South Australia were smaller than those of Kitchener *et al.* (1987). Two size groups were evident (see also Kitchener *et al.* 1987): *Vespadelus finlaysoni* and *V. darlingtoni* were separated from other species by their greater forearm length (Table 1). Females of these two species exceeded 33.0 mm whereas the other three were usually less than 33.0 mm. The three smaller species (*V. regulus*, *V. vulturnus* and *V. baverstocki*) form a species group which is referred to here as the 'regulus complex'.

Within the 'regulus complex' in South Australia there were two subgroups based on forearm length, with a larger species, *V. regulus*, and two smaller species, *V. baverstocki* and *V. vulturnus*. There was considerable overlap in forearm length between *V. baverstocki* and *V. vulturnus*. Among adult females, 90% of *V. regulus* had forearm lengths greater than 30.5 mm, while all *V. vulturnus* and 95% of *V. baverstocki* measured less than 30.5 mm. Fig. 1 shows the overlap in forearm length of females.

TABLE 1. Means and ranges of forearm length (mm) of female *Vespadelus* species in South Australia.

Species	$\bar{x}$	SD	Range	n
<i>V. darlingtoni</i>	35.80 $\pm$ 0.99		(34.7–38.1)	9
<i>V. finlaysoni</i>	34.45 $\pm$ 0.86		(33.0–35.5)	11
<i>V. regulus</i>	31.37 $\pm$ 1.14		(29.3–33.1)	50
<i>V. baverstocki</i>	29.12 $\pm$ 0.95		(27.0–30.9)	38
<i>V. vulturnus</i>	28.47 $\pm$ 1.24		(26.2–30.6)	15

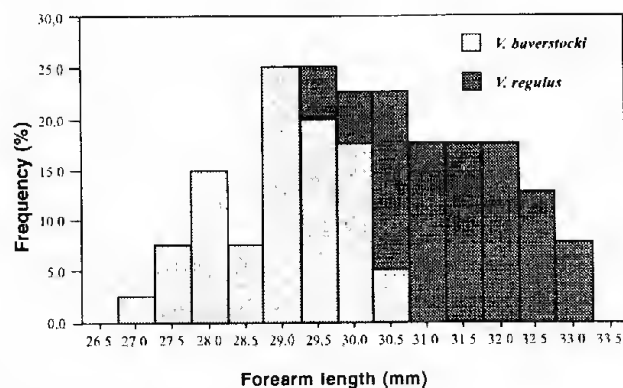


FIGURE 1. Size ranges in forearm length of female *V. baverstocki* and *V. regulus* in South Australia, showing the degree of overlap.

Ratio of Phalanx I: Metacarpal of Digit III

The ratio of phalanx I to the metacarpal on the third wing digit was used by Kitchener *et al.* (1987) to distinguish *V. vulturnus* from other species. Table 2 shows ratio ranges calculated for the three 'regulus complex' species using only specimens identified by electrophoresis. Since sex does not affect this character (Kitchener *et al.* 1987), sexes were combined in the table. The data demonstrate a clear distinction between *V. vulturnus* (ratio ≥ 0.396) and the other two species (ratio ≤ 0.395) and confirm previous findings (Kitchener *et al.* 1987). *Vespadelus baverstocki* and *V. regulus* cannot be distinguished using this ratio.

Distribution and Habitat

Figs 2 to 6 show the geographical distribution of each species. Initially these maps were drawn using only bats that were identified by electrophoresis or penis morphology. Bats identified on wing measurements were examined later and all fell within the distribution ranges already recorded for the species. Habitat information has been taken from Carpenter *et al.* (1978) Reardon and Flavel (1987) and Lumsden and Bennett (1995).

TABLE 2. Range of ratios of phalanx I: metacarpal of digit III of *Vespadelus* spp. of the 'regulus complex' in South Australia. Males and females included.

Species	Ratio	n
<i>V. regulus</i>	0.340–0.395	50
<i>V. baverstocki</i>	0.340–0.395	38
<i>V. vulturnus</i>	0.396–0.420	15

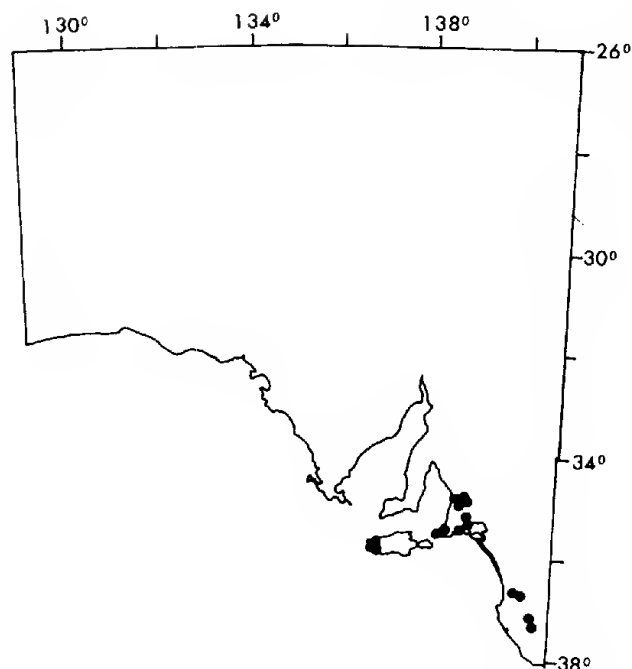


FIGURE 2. Distribution of *V. darlingtoni* in South Australia.

Vespadelus darlingtoni (Fig. 2) is confined to forested areas in the wetter southern and eastern regions of the State;

Vespadelus finlaysoni (Fig. 3) occurs in arid northern areas of South Australia in mountain ranges and rocky country in association with mines and caves;

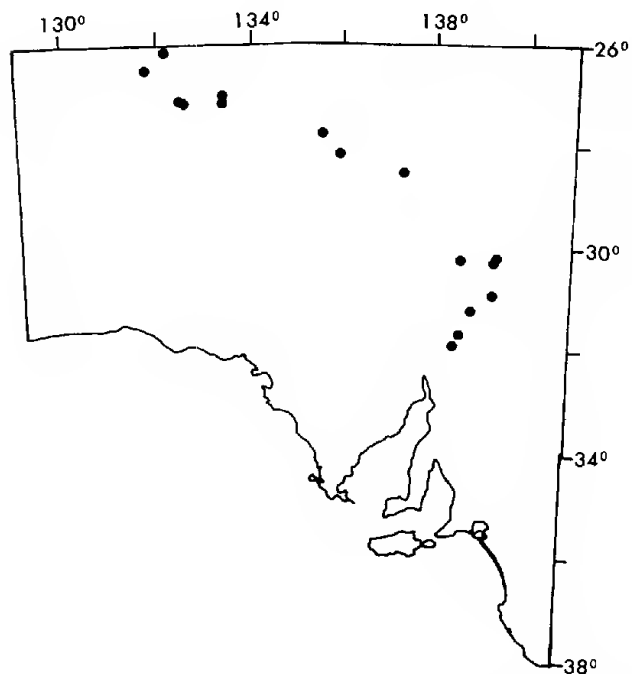


FIGURE 3. Distribution of *V. finlaysoni* in South Australia.

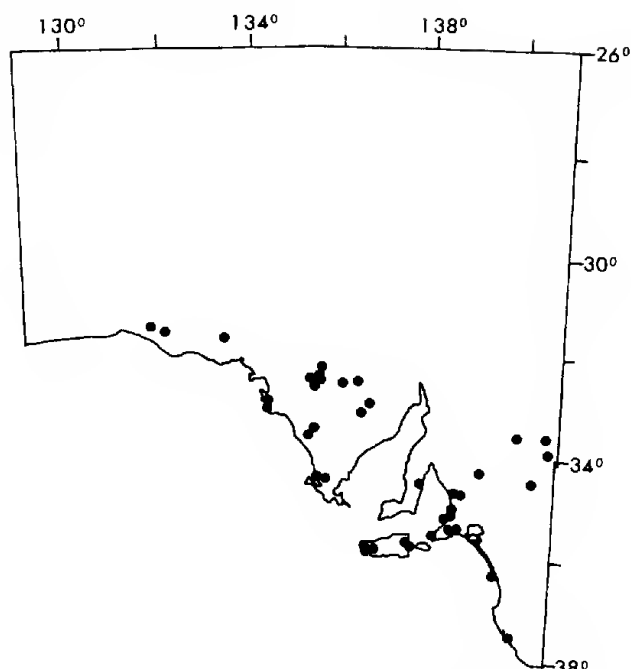


FIGURE 4. Distribution of *V. regulus* in South Australia.

Vespadelus regulus (Fig. 4) occurs in the south and east of South Australia in mallee woodlands and forests. It roosts in tree hollows and buildings. It is the only species found on Yorke and Eyre Peninsula;

Vespadelus baverstocki (Fig. 5) is found over a wide area in the arid and semi-arid woodlands and shrublands of the State and roosts in tree hollows and buildings;

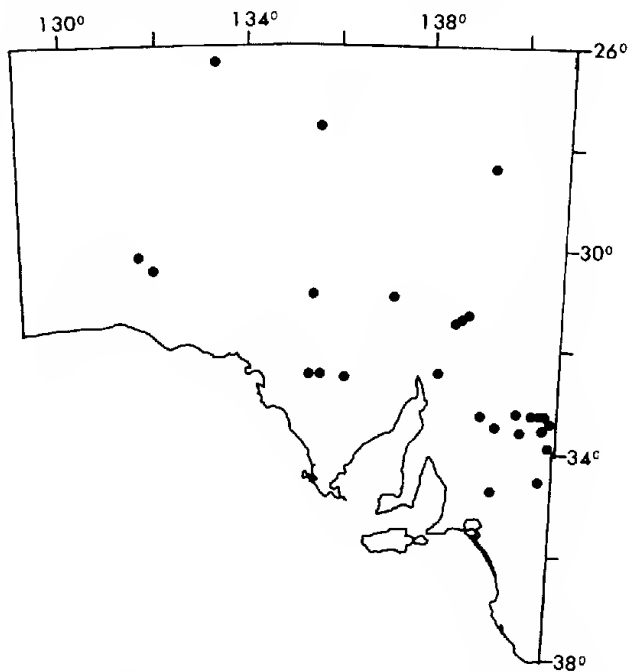


FIGURE 5. Distribution of *V. baverstocki* in South Australia.

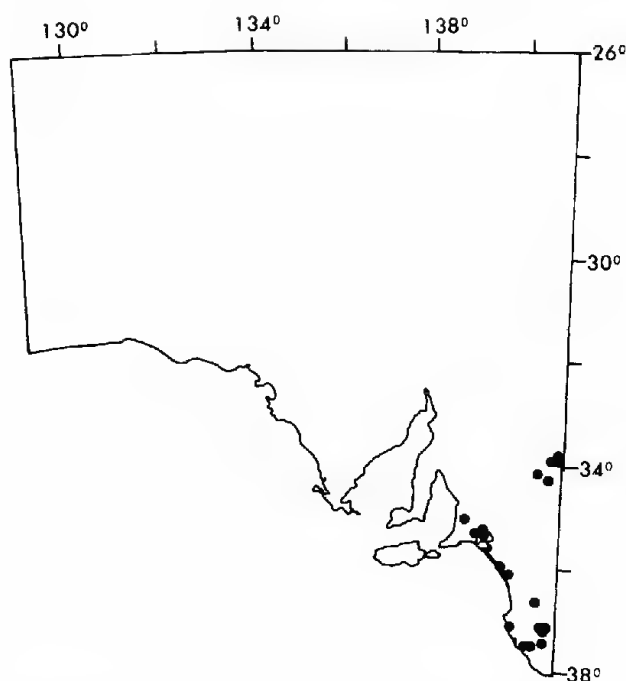


FIGURE 6. Distribution of *V. vulturnus* in South Australia.

Vespadelus vulturnus (Fig. 6) is found in woodlands and forests of the south-eastern region of the State, and along the River Murray. It roosts in tall trees along the River Murray and in the South East (Reardon & Flavel 1987).

Vespadelus regulus and *V. darlingtoni* are the only species of the genus to date recorded on Kangaroo Island.

There are several areas of sympatry for *Vespadelus* species in the State. The range of *V. finlaysoni* is shared with that of *V. baverstocki* (Figs 3 and 5) but the former species is not found in the regions occupied by the other two 'regulus complex' species. The northern limits for *V. regulus* and the southern ranges of *V. baverstocki* overlap in central Eyre Peninsula and the Murray Mallee (Fig. 4). In this region it has been suggested that *V. baverstocki* prefers *Acacia* spp. open woodland and *V. regulus*, the mallee (C. Kemper, T. Reardon pers. comm., Lumsden and Bennett 1995). *Vespadelus vulturnus* inhabits wetter, tall forested areas. Considerable overlap occurs between all three 'regulus complex' species in the River Murray region (Figs 4–6). Here a corridor of sympatry follows the 250 mm isohyet which coincides with the separation of eucalypt (mallee) and *Acacia* spp. woodland (Griffin & MacCaskill 1986) and the well-watered riverine eucalypt forest.

Colour

Differences in fur colour have been noted between *Vespadelus* species (McKean *et al.* 1978; Kitchener *et al.* 1987; Reardon & Flavel 1987). The fur of *V. darlingtoni* is very dark brown, as is the skin on the forearms. By contrast, the fur of *V. finlaysoni* is grey. The 'regulus complex' species share a third colouration type in which the fur is bicoloured, the hairs having brown bases and pale tips. The ventral surface of the body is lighter than the dorsal surface. Hence colour is not useful for distinguishing between the species of the 'regulus complex'.

Electrophoresis

To test the key (below) an additional sample of female bats, with accompanying frozen tissue, was identified using the key as 26 *V. baverstocki*, 10 *V. regulus* and four *V. vulturnus*. Then allozyme electrophoresis was performed on this sample. The allozyme comparisons confirmed that the morphological characters had correctly predicted the identifications of all 40 specimens. This confirmation indicates that despite overlap in some characters, the key can be used with confidence to distinguish the species.

Species summaries

Vespadelus darlingtoni may be easily distinguished from the 'regulus complex' species by its greater size (forearm length) and from *V. finlaysoni* by its dark colour and distribution.

Vespadelus finlaysoni is similarly distinguished by its large size from the 'regulus complex' species. There is a size overlap with *V. regulus* but there is no overlap in distribution.

Vespadelus vulturnus is separated from the two larger species, *V. finlaysoni* and *V. darlingtoni* on size, with no overlap in forearm measurements. A size overlap occurs rarely with *V. regulus* and more commonly with *V. baverstocki* and may be distinguished from these on the basis of the phalanx I: metacarpal ratio.

Vespadelus regulus may be distinguished from *V. darlingtoni* on size and colour, from *V. finlaysoni* on distribution and partly on size, and from *V. vulturnus* partly on size and wing ratios.

Vespadelus baverstocki can be readily distinguished on size from the two largest species, *V. finlaysoni* and *V. darlingtoni*. It can be separated from *V. vulturnus* on the basis of phalanx I: metacarpal ratio. In many cases it can be separated from *V. regulus* on size. When this is not successful electrophoresis must be employed.

KEY TO FEMALE *VESPADELUS* IN SOUTH AUSTRALIA

1. — Forearm greater than 33 mm 2
Forearm less than 33 mm 3
2. — Latitude south of 33°S *V. darlingtoni*
Latitude north of 33°S *V. finlaysoni*
3. — Ratio of phalanx I: metacarpal of digit III greater than 0.39; latitude south of 33°S *V. vulturnus*
Ratio of phalanx I: metacarpal of digit III less than 0.39; locality variable 4
4. — Forearm usually greater than 30.5 mm; mallee habitat/coastal or latitude south of 34°S *V. regulus*
Forearm usually less than 30.5 mm; arid habitat/inland or usually latitude north of 34°S *V. baverstocki*

Note on males

Although males can be identified by penis morphology, this can prove difficult in the field. The characters discussed above can be used to identify males. However my data indicate that male forearms tend to be shorter than females.

TABLE 3. Ranges of forearm length (mm) of male *Vespadelus* species in South Australia.

Species	$\bar{x}$	SD	Range	n
<i>V. darlingtoni</i>	34.9±0.51		(33.5–38.1)	14
<i>V. finlaysoni</i>	33.2±0.64		(32.4–34.4)	13
<i>V. regulus</i>	30.3±0.96		(28.5–33.1)	51
<i>V. baverstocki</i>	29.2±0.96		(26.7–30.7)	29
<i>V. vulturnus</i>	27.7±1.33		(25.2–29.5)	16

Thus the key can be used with some discretion as an aid in identification of males. The one exception is that the identification key and species summaries do not distinguish easily between male *V. regulus* and *V. baverstocki* on forearm lengths (see Table 3).

ACKNOWLEDGMENTS

I wish to thank M. Hutchinson for his advice and encouragement. I am also grateful to K. Bowshall-Hill for drawing the maps. I wish to thank the two referees whose comments greatly improved the final paper, and my husband B. McHenry for encouragement and help in completing the manuscript.

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**FOUR NEW SPECIES OF ANTIPORUS SHARP (COLEOPTERA,
DYTISCIDAE) FROM AUSTRALIA, WITH NOTES ON A. FEMORALIS
(BOH.) AND A. INTERROGATIONIS (CLARK)**

C. H. S. WATTS

Summary

Four new species of *Antiporus* are described from Australia: *A. jenniferae* sp. nov., *A. hollingsworthi* sp. nov., *A. willyamsi* sp. nov. and *A. pembertoni* sp. nov. The distribution of *A. femoralis* (Boh.) and *A. interrogationis* (Clark) in Australia is reviewed. A key to the Australian species is provided.

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C. H. S. WATTS

WATTS, C. H. S., 1997. Four new species of *Antiporus* Sharp (Coleoptera, Dytiscidae) from Australia, with notes on *A. femoralis* (Boh.) and *A. interrogationis* (Clark). *Records of the South Australian Museum* 30(1): 35–42.

Four new species of *Antiporus* are described from Australia: *A. jenniferae* sp. nov., *A. hollingsworthi* sp. nov., *A. willyamsi* sp. nov. and *A. pembertoni* sp. nov. The distribution of *A. femoralis* (Boh.) and *A. interrogationis* (Clark) in Australia is reviewed. A key to the Australian species is provided.

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Manuscript received, 28 February 1996.

The species of *Antiporus* were last revised by Watts (1978) who recognised six species. In 1984 Brancucci (1984) resurrected *A. interrogationis* (Clark) from synonymy with *A. femoralis* (Boh.). In this paper I take the opportunity to describe four additional species of *Antiporus* Sharp from Australia and to review the distribution of *A. femoralis* (Boh.) and *A. interrogationis*. One of the new species, *A. jenniferae*, is close to *A. simplex* Watts, one, *A. willyamsi*, has unusual sexual hairs on the front and middle trochanters and the other two belong to a group of dark coloured *Antiporus* with enlarged metafemora in the males (*A. femoralis*, *A. interrogationis*, *A. wilsoni* Watts, *A. hollingsworthi* n. sp. and *A. pembertoni* n.sp.). Males of this *A. femoralis* group are easily separated on the shapes of the metafemur, proclaw and aedeagus. Females are difficult to distinguish, other than *A. interrogationis* which can be recognised by the colour on the pronotum.

The new species are rare in collections, although this may in part reflect a lack of collecting particularly in south-west Australia.

The collections from which specimens were examined are listed under the following abbreviations:

AM Australian Museum, Sydney.
ANIC Australian National Insect Collection, Canberra.
BMNH Natural History Museum, London.
MV Museum of Victoria, Melbourne.
SAMA South Australian Museum, Adelaide.
WAM Western Australian Museum, Perth.
UQIC Entomology Department Queensland University, Brisbane.

SYSTEMATICS

KEY TO AUSTRALIAN SPECIES OF *ANTIPORUS* SHARP

- 1 — Protarsus with 2 claws Females 2
— Protarsus with 1 claw Males 10
- 2 — Relatively large (> 6mm), predominantly reddish-yellow, elytra with 5–6 often incomplete long dark lines *A. gilberti* (Clark)
— Not with above combinations of characters 3
- 3 — Protarsi black. Relatively small (<4mm) ..
..... *A. jenniferae* sp. nov.
— Protarsi reddish-yellow, same colour as rest of leg 4
- 4 — At least the basal segment of mesotarsi enlarged in comparison with protarsi 5
— Segments of mesotarsi similar to those on protarsi or smaller 6
- 5 — Elytron with small and large punctures, all mesotarsal segments larger than those of protarsi, elytra with lighter streaking in younger specimens ... *A. willyamsi* sp. nov.
— Elytra with uniform punctuation, only basal segment of mesotarsi enlarged, elytra uniformly dark red-brown to black .
..... *A. wilsoni* Watts
- 6 — Smaller (< 3.5mm) 7
— Larger (>3.5mm) 8

- 7 — Elytron dark, usually with three reddish-yellow spots, pronotum reddish-yellow with dark front and rear borders *A. bakewelli* (Clark)
 — Elytron and pronotum uniformly red-brown *A. simplex* Watts
- 8 — More or less uniformly dark reddish-brown, elytron tip often appears truncated *A. blakei* (Clark)
 — Elytra normally black with or without lighter markings. Tip of elytron pointed . 9
- 9 — Black portion in centre of pronotum not reaching front border *A. interrogationis* (Clark)
 — Black portion in centre of pronotum reaching front border
 *A. hollingsworthi* sp. nov. (W.A. only),
 ?*A. pembertonii* sp. nov. (W.A. only, female unknown), *A. femoralis* (Boh.)
- 10 — Prominent cup-like tuft of long golden setae on mesotrochanters (Fig. 28). Segments of mesotarsus larger than segments of protarsi
 *A. willyamsi* sp. nov.
 — Mesotrochanters without such a tuft of setae. Segments of mesotarsus smaller than those of protarsi 11
- 11 — Metafemur produced on inside near apex 12
 — Metafemur simple 13
- 12 — Relatively large (>6 mm), predominantly reddish-yellow, elytron with several long black lines. Metafemur with prominent narrow triangular process on inside near apex *A. gilberti* (Clark)
 — Predominantly dark-brown to black. Metafemur broadly produced on inside near apex 16
- 13 — Larger (length > 4.5 mm). Mesotibia strongly triangularly produced in middle on outside *A. blakei* (Clark)
 — Smaller (length < 3.7 mm). Mesotibia simple or thickened and angular but never as above 14
- 14 — Protarsi black in contrast to red-brown colour of rest of leg
 *A. jenniferae* sp. nov.
- Protarsi reddish-brown, same colour as rest of leg 15
- 15 — Elytron unicolorous, except for slightly paler sutural region and sides. Metacoxal lines evenly diverging anteriorly. Claw on protarsus relatively straight, with small basal tooth (Fig. 21)
 *A. simplex* Watts
 — Elytron with one or more pale patches. Metacoxal lines much less divergent in anterior quarter than in middle. Claw on protarsus sickle-shaped, with large basal tooth (Fig. 18) *A. bakewelli* (Clark)
- 16 — *A. femoralis* complex. The species are best separated by characters of the aedeagus and metafemur given in Figs 1–15. In addition the black portion in the centre of the pronotum does not reach the front border in *A. interrogationis* whereas it does in the other species.

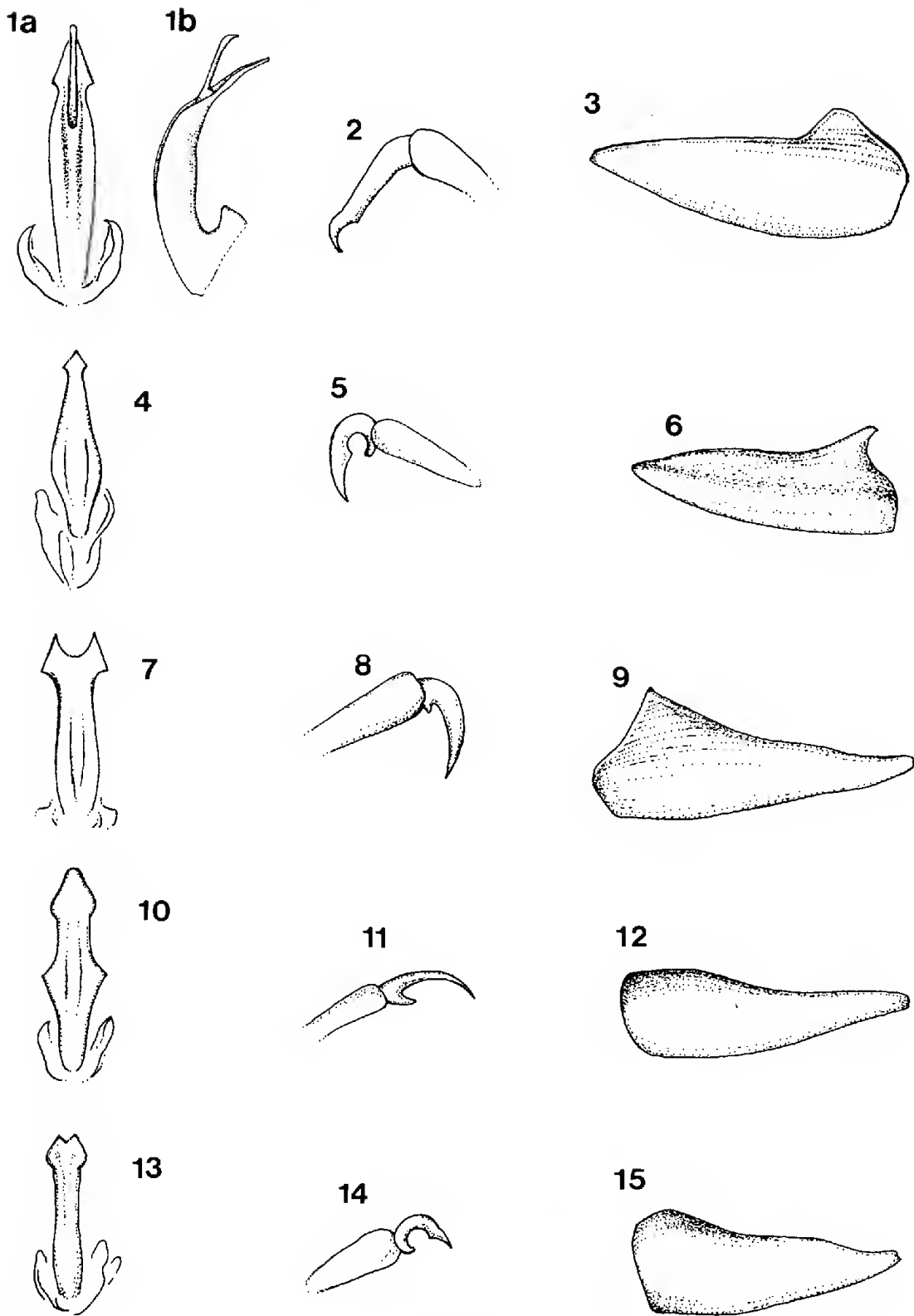
Antiporus femoralis (Boheman, 1858)
 (Figs 7, 8 & 9)

Number examined, 83.

Brancucci (1984) clarified the relationships between this widespread and common species and *A. interrogationis* (Clark). It can be separated from this species by characters of the aedeagus and metafemur and in having the dark patch on the middle part of the pronotum reaching the anterior border. In this last character it is similar to the other members of the *A. femoralis* group. It differs from these in characters mentioned under the different species and illustrated in the figures.

Distribution

Australian Capital Territory: Black Mountain, ANIC; Hackett, ANIC; Mt Coree, ANIC; O'Connor, ANIC. **New South Wales:** Allyn River, ANIC; Galston, ANIC; Queanbeyan, ANIC; Sydney, MV, ANIC; Waratah, SAMA; Williams River, ANIC. **South Australia:** Beachport, AM; Eyre Peninsula, SAMA; Kangaroo Island, SAMA; Lucindale, SAMA; Port Lincoln, AM, SAMA. **Tasmania:** 11 km NNW Blackland, ANIC; Eaglehawk Neck, AM; Georgetown, MV; Hobart, MV; Launceston, MV; Liffey Valley, ANIC; Waldheim, UQIC. **Victoria:** 4 km W. Ballan, MV; L. Barracoota, MV; Cape Otway, MV; 10 km NW Dartmouth Dam, MV; La Trobe, SAMA; L. Lcarmonth, ANIC; 10 km NW



FIGURES 1–15. 1a, dorsal view of aedeagus of *A. hollingsworthi*; 1b, lateral view of aedeagus of *A. hollingsworthi* showing apical appendage; 2, proclaw of male *A. hollingsworthi*; 3, postfemur of *A. hollingsworthi*. 4, dorsal view of aedeagus of *A. interrogationis*; 5, proclaw of male *A. interrogationis*; 6, postfemur of *A. interrogationis*. 7, dorsal view of aedeagus of *A. femoralis*; 8, proclaw of male *A. femoralis*; 9, postfemur of *A. femoralis*. 10, dorsal view of aedeagus of *A. pembertoni*; 11, proclaw of male *A. pembertoni*; 12, postfemur of *A. pembertoni*. 13, dorsal view of aedeagus of *A. wilsoni*; 14, proclaw of male *A. wilsoni*; 15, postfemur of *A. wilsoni*.

Lexton, MV; Montmorency, SAMA; Mt Buffalo, MV; Mudgee, ANIC; Myrtleford, MV; Oakleigh, MV; Reservoir, MV; Werribee, MV. **Western Australia:** 9 mi NE by E Esperance, ANIC; Geraldton, MV; King George Sound, ANIC; Mullewa, SAMA; Ravensthorpe, ANIC; Stirling National Park, ANIC; Swan River, SAMA; Wilga, ANIC.

Antiporus interrogationis (Clark, 1862)
(Figs 4, 5 & 6)

Number examined, 62.

As pointed out by Brancucci (1984), *A. interrogationis* is clearly distinct from *A. femoralis* with which I had previously synonymised it (Watts 1978). Apart from the aedeagus (Fig. 4) and metafemur (Fig. 6), *A. interrogationis* differs from the other members of the *A. femoralis* group by the dark patch on the middle part of the pronotum usually not reaching the anterior border.

Distribution

Australian Capital Territory: Black Mountain, ANIC; Paddy's River, ANIC. **New South Wales:** 37 km E Hay, SAMA. **South Australia:** Naracoorte, UQIC. **Victoria:** 4 km W Ballan, MV; Bright, SAMA, MV, AM; Buninyong, MV; Delatite, MV; Delley's Dell Grampians, SAMA; Dividing Range, SAMA; Eltham, MV; Glen Valley, MV; Hamilton, MV; L. Purrumbete, MV; L. Wendouree, MV; Linga, MV; Melbourne, ANIC, MV; Merrimans Creek, MV; Mitta Mitta River, MV; Montmorency, SAMA; Mt Buffalo, SAMA; Nelson, SAMA; Noorinbee North, MV; Six Mile Creek Dartmouth, MV; 8 km NE Toolangi, MV; Warburton, MV; Werribee, MV; Yarra River, MV; Yarrawonga, MV.

Antiporus jenniferae sp. nov.
(Figs. 25, 26 & 27)

Description (number examined 63).

Length 3.4–3.6 mm. Oblong-oval, convex, widest behind middle, elytron somewhat elongate posteriorly, tip sharp. Reddish yellow, portions of elytra a bit darker, sutural lines narrowly darker and bordered with pale strip, apical portions lighter; protarsi darker almost black in some specimens. Strongly, densely, and evenly punctured throughout. Pronotum and clytron

narrowly margined, clytron moderately serrate towards apex, except for short distance near tip. Apical segments of both maxillary and labial palpi weakly bifid at tips. Prothoracic process narrowly lanceolate, rounded, almost keeled in cross section, slightly narrowed between procoxae. Metacoxal lines raised, moderately separated, diverging slightly posteriorly, widening to about twice their narrowest width anteriorly. Some long setae arising from pit in centre of sternite numbers three and four. A line of long setae towards sides of elytron.

Male: Pro- and mesotarsi moderately expanded, first and second segments as long as wide, claw on protarsus thickened, strongly bent near base, abruptly narrowing to sharp point at apex, with large basal tooth. Mesotibia robust, broadly but weakly indented on inner side in middle. Seta tufts on mesotrochanters somewhat thicker than on female.

Female: Mesotarsi a little expanded, protarsi less so. Protarsus with two simple claws.

Remarks

A. jenniferae can be distinguished from all other *Antiporus* by its relatively small size, and its black protarsi. It appears closest to *A. simplex* and *A. bakewelli*. From *A. simplex* it differs by its black protarsi, elytral colour pattern which although less marked than in *A. bakewelli* is clearly present, the aedeagus having a broader tip and widening slightly in the middle compared with the more parallel-sided aedeagus in *A. simplex* and the spine at the base of the claw on the male protarsi being larger than in *A. simplex*. Based on the small numbers of specimens of both species available it appears to be a little larger. From *A. bakewelli* it differs in its black protarsi, less marked and more diffuse elytral colour pattern, the aedeagus with a broader tip, and the claw on the male protarsi being straighter in comparison with the smoothly sickle-shaped claw of *A. bakewelli*.

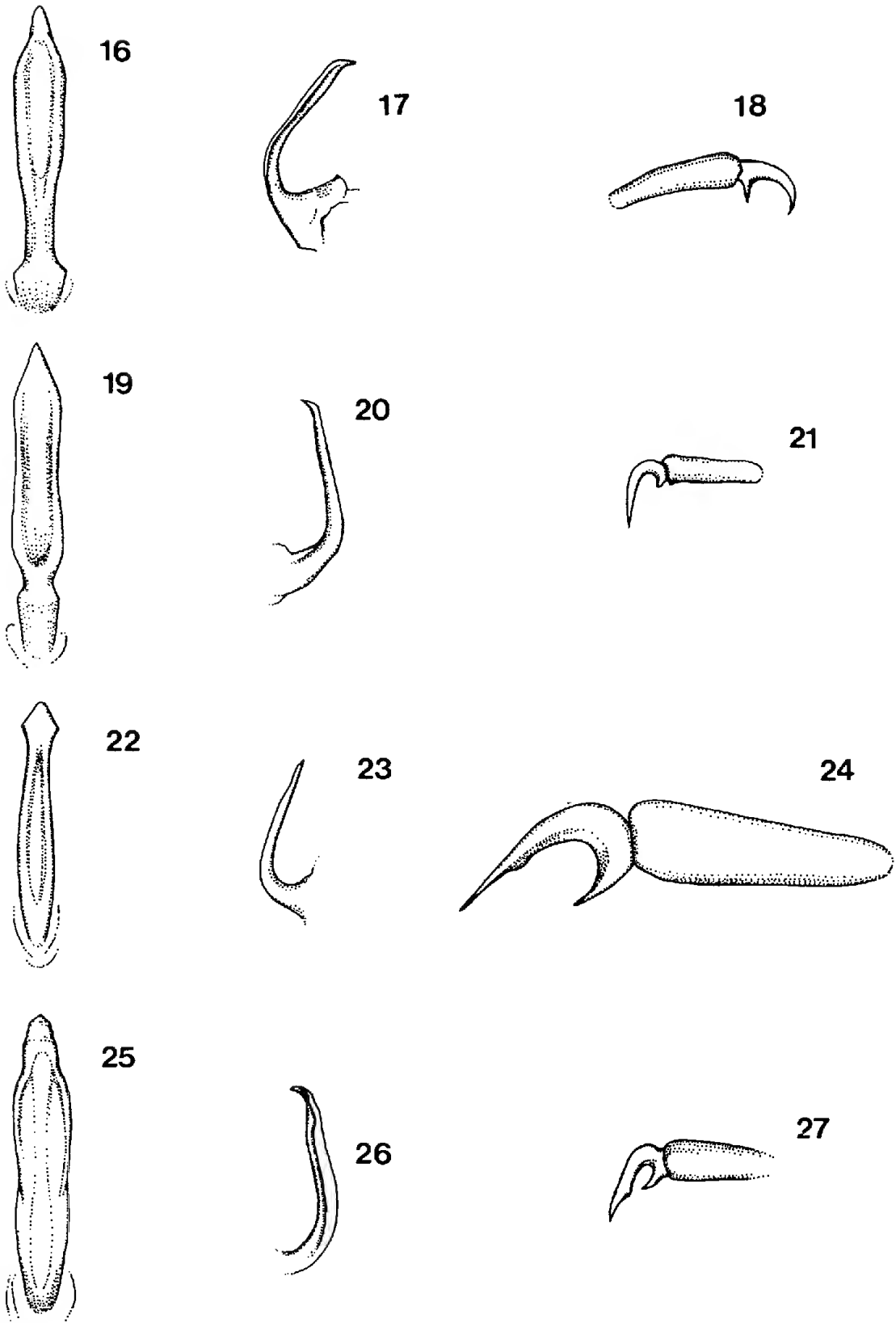
Distribution

Most specimens are from Cape York Peninsula, but it is also known from Adelaide River, N.T. (in BMNH) and Synnot Creek in northern W.A. (in ANIC).

Types

Holotype male: "25K. N. Coen Qld. 29/9/84 C. Watts" in SAMA.

Paratypes: 1, "12.40S 142°40E Qld Batavia Downs Hmsd. 17–23 Jun. 1992 T.A. Weir, at



FIGURES 16–27. 16 & 17, dorsal and lateral view of aedeagus of *A. bakewelli*; 18, lateral view of male *A. bakewelli* proclaw. 19 & 20, dorsal and lateral view of aedeagus of *A. simplex*; 21, lateral view of male *A. simplex* proclaw. 22 & 23, dorsal and lateral view of aedeagus of *A. willyamsi*; 24, lateral view of male *A. willyamsi* proclaw. 25 & 26, dorsal and lateral view of aedeagus of *A. jenniferae*; 27, lateral view of *A. jenniferae* proclaw.

light", in ANIC; 2, "12.40S 142.40E Batavia Downs Qld 03–10 Mar 1993 at light, I. Cunningham", in ANIC; 1, "16.31S 126.1E CALM site 25/1 Synnot Ck W.A. 17–20 June 1988 T.A. Weir", in ANIC; 11 "25k N. Coen Qld 29/9/85 C. Watts", in SAMA; 1, "24M.S. Musgrave N.Q. 20.5.72 J.C. Brooks at light", in ANIC; 1, "13.34S 142.32 E Qld, 17 km N.W. by W. of Rokeby (Vardons Lagoon) 27 Oct. 1992, T. Weir, P. Zborowski, Small pool with debris", in ANIC; 56, "Qld Mt. Molloy 2 km S. 30/3/96, C. Watts", in SAMA.

***Antiporus pambertonii* sp. nov.**
(Figs 10, 11 & 12)

Description (number examined 1).

Length 4.6mm. Oblong oval, dark red brown – black, front of head, sides of pronotum broadly and sides of elytron narrowly but diffusely light-testaceous. Ventral surface testaceous, sides of meso and metasterna darker, apical tips of metatibiae darker. Dorsal surface rather finely punctured, stronger laterally, punctures on head a little smaller than eye facets, punctures at rear of pronotum towards sides and on adjacent areas of elytra tending to join in roughly longitudinal lines. Ventral surface much more strongly punctured, strongly rugose-punctate laterally. Pronotum narrowly but clearly margined, elytron weakly so. Prothoracic process narrow, strongly raised, sides sub-parallel, bluntly tipped. Metacoxal lines well separated, sub-parallel in posterior third and anterior quarter, diverging in between so that anteriorly about twice the distance apart as posteriorly, area between coxal lines and forward onto mesosternum depressed.

Male: Protarsi moderately expanded, protarsal claw large, slender, with well developed slender basal tooth. Mesotibia weakly indented on inner margin towards apex. Metafemur broadly expanded on inner edge at apex, some strong punctures and weak longitudinal ridging on expanded area.

Female: Unknown

Remarks

More weakly punctured than the other species in the *A. femoralis* complex, with the large punctures along the front of the pronotum distinct and more than twice the size of others on the pronotum. Characters of the male aedeagus and metafemur are diagnostic. Known only from a single specimen I collected in a small stream in cleared land near Pemberton.

Distribution

Known only from unique type from near Pemberton, S.W. Australia.

Type

Holotype male: "W. Aust. 15 km N.W. Pemberton, 17 May 1987, C. Watts" in SAMA.

***Antiporus hollingsworthi* sp. nov.**
(Figs 1, 1a, 2, & 3)

Description (number examined 15).

Length 4.1–4.6mm. Oblong oval, convex. Dark red-brown, appendages lighter. Strongly evenly and densely punctate throughout, punctures smaller on head than elytra, punctures at rear of pronotum towards sides and on adjacent areas of elytra tending to join in linear longitudinal lines, punctures towards sides of metacoxae and sternites and on elytral epipleura very close together and tending to coalesce. Pronotum and elytra narrowly margined except for short distance at tips of elytra, lacking serration, sides of elytra before apex appear weakly and broadly flanged from some angles. Prothoracic process narrow, blunt, strongly carinate. Metacoxal lines sub-parallel in anterior and posterior third, rapidly diverging in middle.

Male: Pro- and mesotarsi moderately expanded. First and second segments wider than long. Claw on protarsus strongly bent near base, straight with parallel sides in middle, rapidly narrowing at apex basal tooth subobsolete. Mesotibia a little thickened, weakly and broadly indented on inner edge in middle. Apical ventral edge of mesofemur expanded a little. Inner ventral edge of metafemur with large, broad, triangular expansion in apical third. Parameres robust, broad, aedeagus arrow-headed with thin protuberance above tip arising from neck of arrow.

Female: Pro- and mesotarsi a little expanded; claws, meso- and metafemur and tibia simple.

Remarks

Antiporus hollingsworthi is a member of the *A. femoralis* group. It appears closest to *A. wilsoni* from the south-east of Australia which it resembles in the pronotal and elytral grooving, thickened male mesotibia and expanded metafemur.

Antiporus hollingsworthi can be separated from both *A. femoralis* and *A. interrogationis* by the lack of pronounced paler areas on the head, pronotum and elytra, although some specimens of

A. hollingsworthi do have head, pronotum and elytral patches paler than the rest of the upper surface. The tendency of the punctures on the rear edge of the pronotum and the adjacent areas on the elytra to link up and form grooves is more pronounced than in either *A. femoralis* or *A. interrogationis* and the triangular expansion on the male metafemur is more rounded than in either of these species. *A. femoralis* and *A. interrogationis* also lack the thickened and indented mesotibia present in *A. hollingsworthi*, *A. wilsoni* and to a lesser extent in *A. pembedtoni*. *Antiporus hollingsworthi* is more strongly punctured than *A. pembedtoni* and the males have differently shaped metafemora (Fig. 3). It differs from *A. wilsoni* by characters of the aedeagus, by the indentation on the male mesotibia being more central, and in having a triangular rather than a rounded expansion to the male metafemur. *Antiporus hollingsworthi* differs from all other *Antiporus* species (and all Australian Dytiscidae) by the apical appendage on the aedeagus.

Distribution

So far *A. hollingsworthi* is known only from Perth and Carrington, W.A. and from two unlocalised localities in the South-west. However, of all the Australian regions this is the most poorly sampled for water beetles so it is likely to be more abundant than the few known specimens indicate.

Types

Holotype male: "W. Aust. Maidavale, 27th April 1990, C. Watts", in SAMA.

Paratypes: 1 male, 7 females, same data as Holotype, in SAMA; 1 female "Perth 10/65 DE", in SAMA; 1 female "S.W.A. ?Rotnest, Edward", in SAMA; 1 male "JT201", in SAMA; 1 male, 1 female "R.P. McMillan, Carrington, 19.7.53", in WAM.

Etymology

Named after Rod Hollingsworth, a strong supporter of Natural History at the South Australian Museum.

Antiporus willyamsi sp. nov.
(Figs 22, 23, 24 & 28)

Description (number examined 4).

Length 3.4–3.6 mm. Oblong-oval. Widest behind middle. Testaceous, head, lateral quarters of pronotum, patches on elytra and appendages

lighter, metafemur and tibia tend to be a little darker towards their apices, lighter patches on elytron tending to form broad longitudinal streaks. Strongly, densely and evenly punctate, punctures on discs of pronotum and head weaker, particularly on head, a few scattered much smaller punctures on disc of pronotum and elytra. Pronotum narrowly but distinctly margined, elytra less so. Prothoracic process with central keel, narrow between procoxae. Metacoxal lines raised, sub-parallel in posterior half and anterior quarter, diverging in between, about twice the distance apart anteriorly compared with posteriorly, reaching mesofemur. Some long setae arising from pits in centre of sternites three and four, and a line of long setae on dorsal surface of elytron close to side.

Male: Protarsi expanded, second segment broadest, mesotarsi strongly expanded, first and second segments largest, sub-equal. Mesofemur and mesotibia stouter than profemur and protibia. Protarsus with single claw, strongly bent, long and narrow, with well developed basal tooth and weak bulbous area in middle. Protochanters with well marked cup-like tuft of golden setae, mesotrochanters with a much larger scallop-shaped tuft of similar setae. Metafemur stout, ventral inner apical region with scattered large punctures and about four longitudinal grooves/ridges.

Female: Protarsus with two weak claws. Mesotarsi moderately expanded, first and second segments largest, sub-equal. Mesotibia stout.

Remarks

The species is easily recognised by the spectacular development of the setae on the trochanters of the male which is unlike anything I

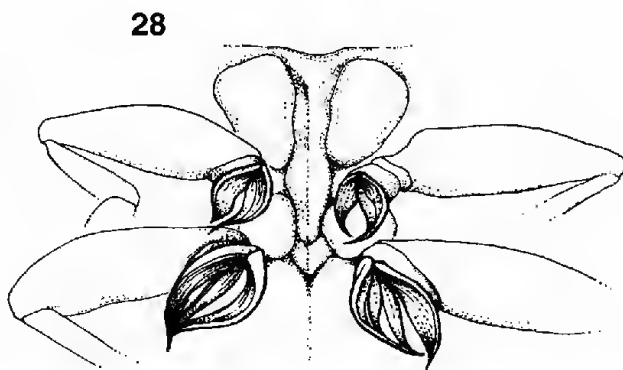


FIGURE 28. Meso- and metatrochanters of *A. willyamsi*.

have seen on other beetles. The very broad mesotarsi in the male and the striped elytral colour pattern in teneral individuals are also distinctive.

Since collecting the original specimens in 1983, I have revisited the locality (a deep, narrow, spring-fed drainage ditch in acidic soil) a number of times without success. Biologically the area has now changed considerably from a healthy habitat with numerous species to one that is almost devoid of insect life although physically little changed.

Distribution

Known only from the type locality in the south-east of South Australia and from Healesville, Victoria.

Types

Holotype male: "10 km S. Robe, S.A., 1/83, C. Watts", in SAMA.

Paratypes: 2 females, same data as holotype, in SAMA; 1 female, "Healesville, V. 12/68, C. Watts", in SAMA.

CHECKLIST OF AUSTRALIAN *ANTIPORUS* SHARP

A. bakewelli (Clark, 1862)
A. blakei (Clark, 1862)
A. femoralis (Boheman, 1858)
A. gilberti (Clark, 1862)
A. hollingsworthi sp. nov.
A. jenniferae sp. nov.

A. pembertoni sp. nov.
A. simplex Watts, 1978
A. willyamsi sp. nov.
A. wilsoni Watts, 1978
A. interrogationis (Clark, 1862)

ACKNOWLEDGMENTS

The curators of the collections listed earlier are thanked for allowing me to examine specimens in their care. Mrs Vicki Wade typed the manuscript and Mr R. Gutteridge drew the illustrations. All these are thanked for their support and help.

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THYLACINUS MEGIRIANI, A NEW SPECIES OF THYLACINE (MARSUPIALIA: THYLACINIDAE) FROM THE ONGEVA LOCAL FAUNA OF CENTRAL AUSTRALIA

PETER F. MURRAY

MURRAY, P. F. 1997. *Thylacinus megiriani*, a new species of thylacine (Marsupialia: Thylacinidae) from the Ongeva Local Fauna of Central Australia. *Records of the South Australian Museum* 30(1): 43–61.

Approximately 10% larger than a maximum-sized Tasmanian wolf, the late Miocene/early Pliocene *Thylacinus megiriani* n. sp. exhibits some similarities to the late Miocene thylacinid, *T. potens* Woodburne 1967 and early to mid-Miocene *Nimbacinus dicksoni* Muirhead and Archer 1990, while simultaneously expressing several derived features in common with the Recent thylacine, *T. cynocephalus*. Other than the presence of a tiny styler cusp-like structure distal to styler cusp D on M^3 , which could be an artefact of wear, *T. megiriani* shows no definite uniquely derived characters that would exclude it from ancestry of the recently extinct *T. cynocephalus*.

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Fossil vertebrates were first described from the Alcoota Local Fauna at Alcoota (Fig. 1), northeast of Alice Springs, by Woodburne (1967). The stratigraphically superposed Ongeva Local Fauna contains certain taxa that are more derived than those from the nearby Alcoota Local Fauna (Murray, Megirian & Wells 1993, Megirian, Murray & Wells 1996). Among its characteristic species is a zygomaticurine diprotodontid, *Kolopsis yperus* Murray, Megirian & Wells, which is probably synonymous with the Cheltenhamian-aged *Zygomaticurus gilli* Stirton 1967. *K. yperus* is more similar to *Zygomaticurus* species than is the Alcoota Local Fauna species *Kolopsis torus* Woodburne 1967. *Thylacinus megiriani* appears to be analogously derived in comparison to the Alcoota Local Fauna thylacine, *T. potens*.

A direct ancestor of *T. cynocephalus* has not been identified. *T. rostralis*, *T. spelaeus* and *T. major* are considered to be synonymous with *T. cynocephalus* (Dawson 1982). Other thylacinids are considered to be too primitive or too specialised (Archer 1982, Muirhead & Archer 1990, Muirhead 1992, Wroe pers. com.). Ambiguity in the homology of the posterior styler cuspules on the molars of *T. cynocephalus* has resulted in a less than definitive resolution of late Tertiary thylacinid phylogeny. *T. megiriani* provides some additional evidence pertaining to the homology of the cusps and some hypotheses of the phylogeny of the recent species of *Thylacinus* are discussed.

MATERIALS AND METHODS

As is often the case with Ongeva LF fossils, NTM P9618 is not an ideal specimen, having been found in a number of pieces scattered throughout a hard nodule of calcareous sandstone. As fragments were extracted more or less individually, including fragments of the molar teeth, the specimen was glued together at the excavation site along what appeared to be the likely contacts. The fragile condition of the specimen dictated that several coats of Synocryl (Bodacryl) be applied to harden and hold it together securely. However, this compound sometimes has the disadvantage of obscuring important morphological details, particularly when fine particles of the matrix become incorporated with the solution, sometimes suppressing surface detail and occasionally even mimicking small structures.

So it was with this specimen, that certain features of the restoration seemed untenable, such as a slight overlap of the P^2 alveolus with that of the P^1 . As *Thylacinus potens* has no appreciable diastema between these teeth, this arrangement appeared to be plausible, though further cleaning of the matrix and excess Synocryl from the specimen, in response to an observation by one of the referees, proved that it had not been restored correctly. This revelation provoked a more radical program of disassembly and cleaning of the specimen which I was initially afraid to attempt

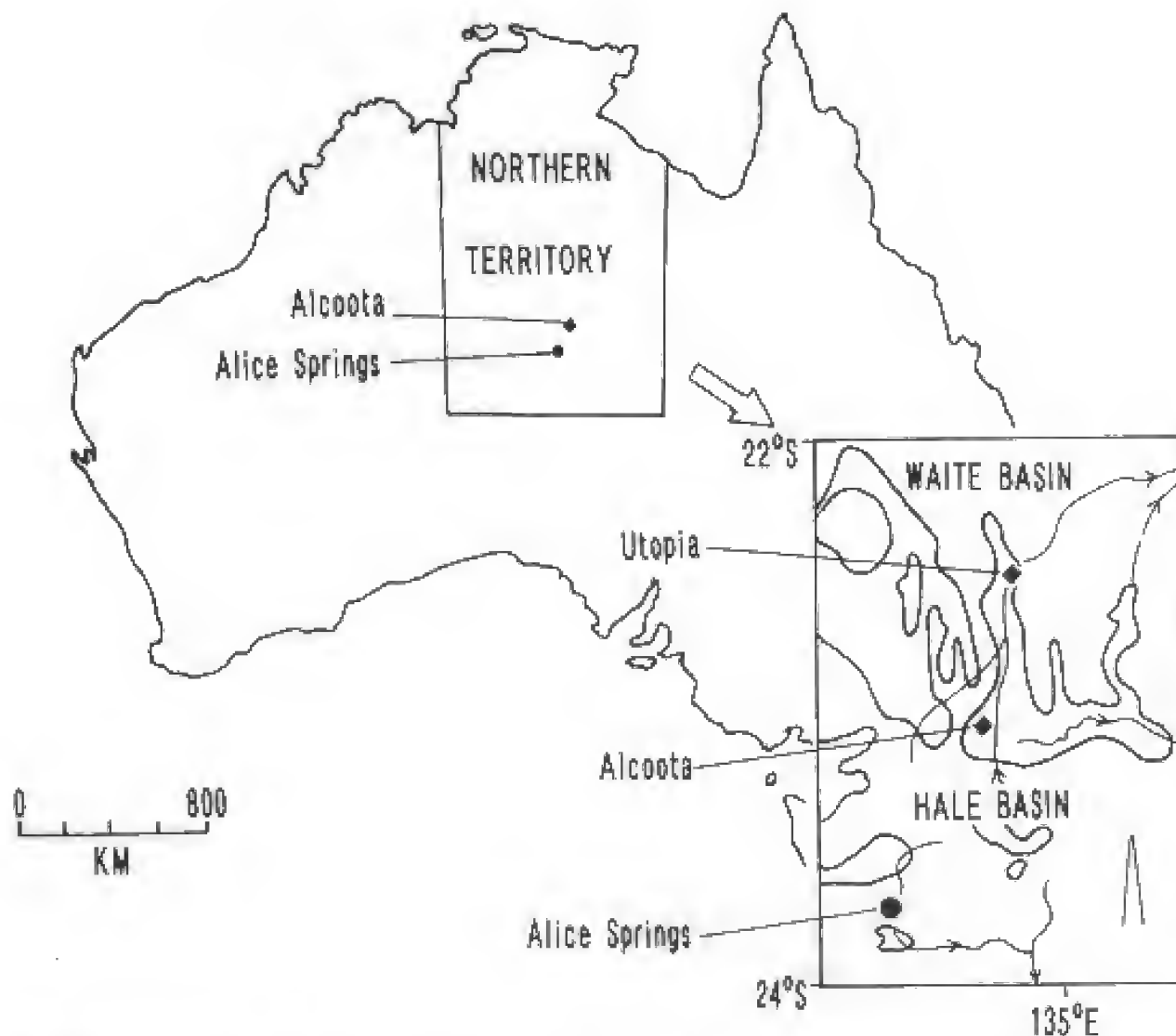


FIGURE 1. Locality map; the Ongeva LF is located on Alcoota Station, near Alice Springs Northern Territory.

due to its extreme fragility. The new restoration has greatly improved the resolution of the specimen, to the extent that many of my initial observations can be stated more confidently; though as will be discussed, some features of the specimen remain equivocal.

As the first draft of this paper was based on the original restoration, I have briefly described and illustrated the modifications I made to the specimen to avoid confusion with any errant copies of the earlier manuscript. I am extremely grateful to my referees for alerting me to the possibility that the specimen might be distorted, and for drawing to my attention several other morphological features, resulting, I believe, in a much improved account of the species.

SYSTEMATICS

Family THYLACINIDAE Bonaparte 1838

Thylacinus megiriani n. sp.

Holotype

NTM P9618 (field ref. no. SQ107), left maxilla with P^1 , P^3 , M^{1-3} .

Type locality

Hill 1, South Quarry, approximately 2 km southwest of the junction of Ongeva and Waite Creeks, Alcoota Station, Northern Territory, latitude $22^{\circ}52'S$, longitude, $134^{\circ}27'E$. The Type

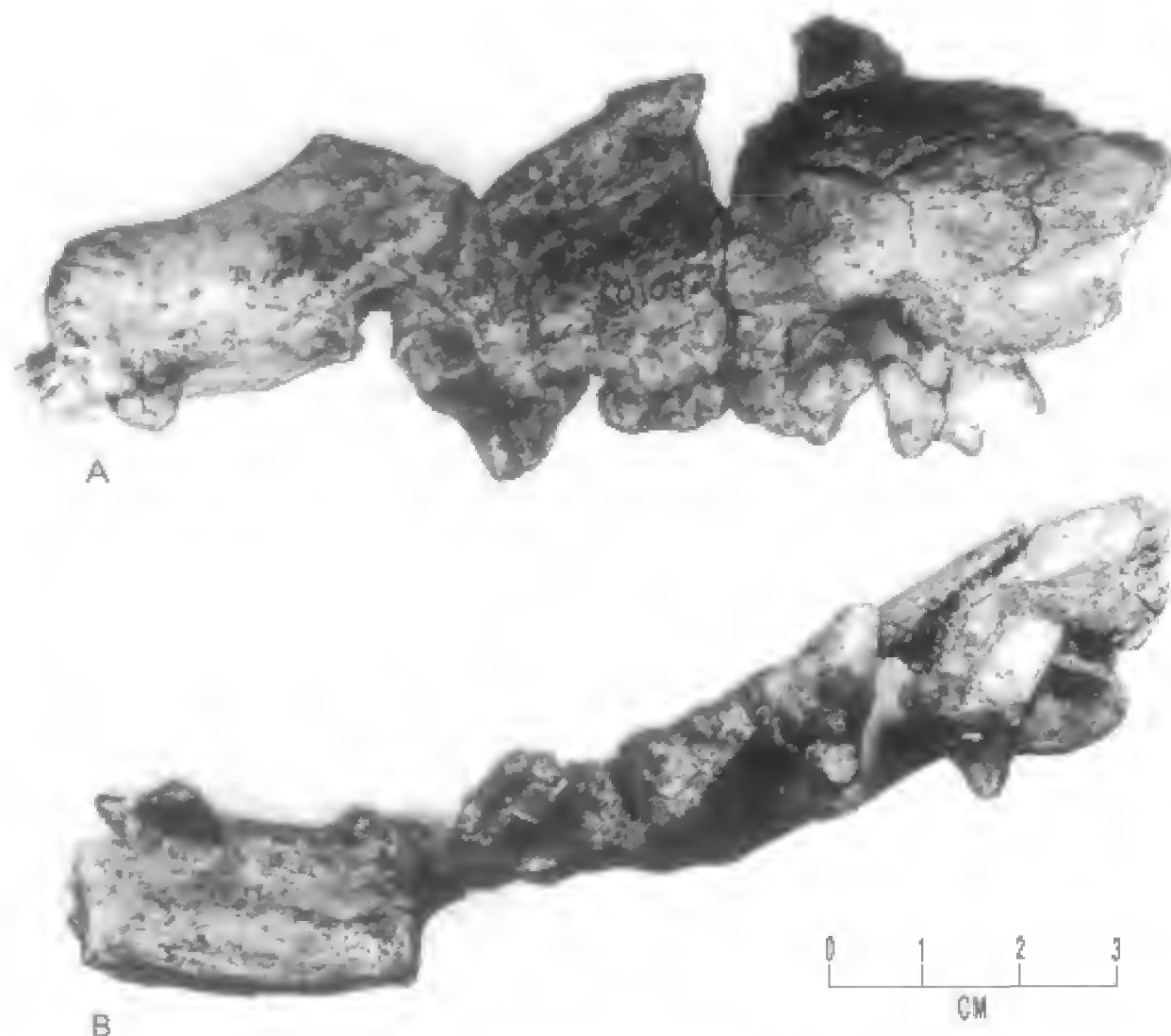


FIGURE 2. Photograph of the left maxilla of *Thylacinus megirianii* n. sp. (NTM P9618); A, lateral aspect; B, palatal aspect. This photograph depicts the field restoration of the specimen in which the fragment containing P¹ and P² had been glued approximately 8.0 mm posterior to its correct position, leading to the initial impression that the posterior root of P² was adjacent to, or slightly overlapped that of P³. Note also that the M¹ is twisted medially (B) and is nearly a centimetre out of alignment with M².

was recovered from a sandy siltstone channel deposit in the Waite Formation, approximately 10m above the fossiliferous lacustrine sediments containing the Alcoota Local Fauna (Murray, Megirian & Wells 1993, Megirian, Murray & Wells 1996), (Fig. 1).

Fauna

Ongeva Local Fauna (Murray *et al.* 1993).

Rock unit and age

Waite Formation, Cheltenhamian equivalent, late Miocene-?early Pliocene.

Specific diagnosis

A large, long-snouted thylacinid, equal to, or larger than *T. cynocephalus* but less massive than *T. potens*; much larger than *N. dicksoni* (Muirhead and Archer 1990) and *T. macknessi* (Muirhead 1992). P¹⁻² shorter and narrower than in *T. potens*; P¹ in line with P²⁻³, contrasting with *T. potens* in which P¹ is obliquely oriented and situated medial to the midline of the canine alveolus. P³ large as in *T. potens*. Premolar diastemata longer than in *T. potens* and in *Nimbacinus dicksoni*, more comparable to *T. cynocephalus*. M¹⁻³ longer and narrower than in

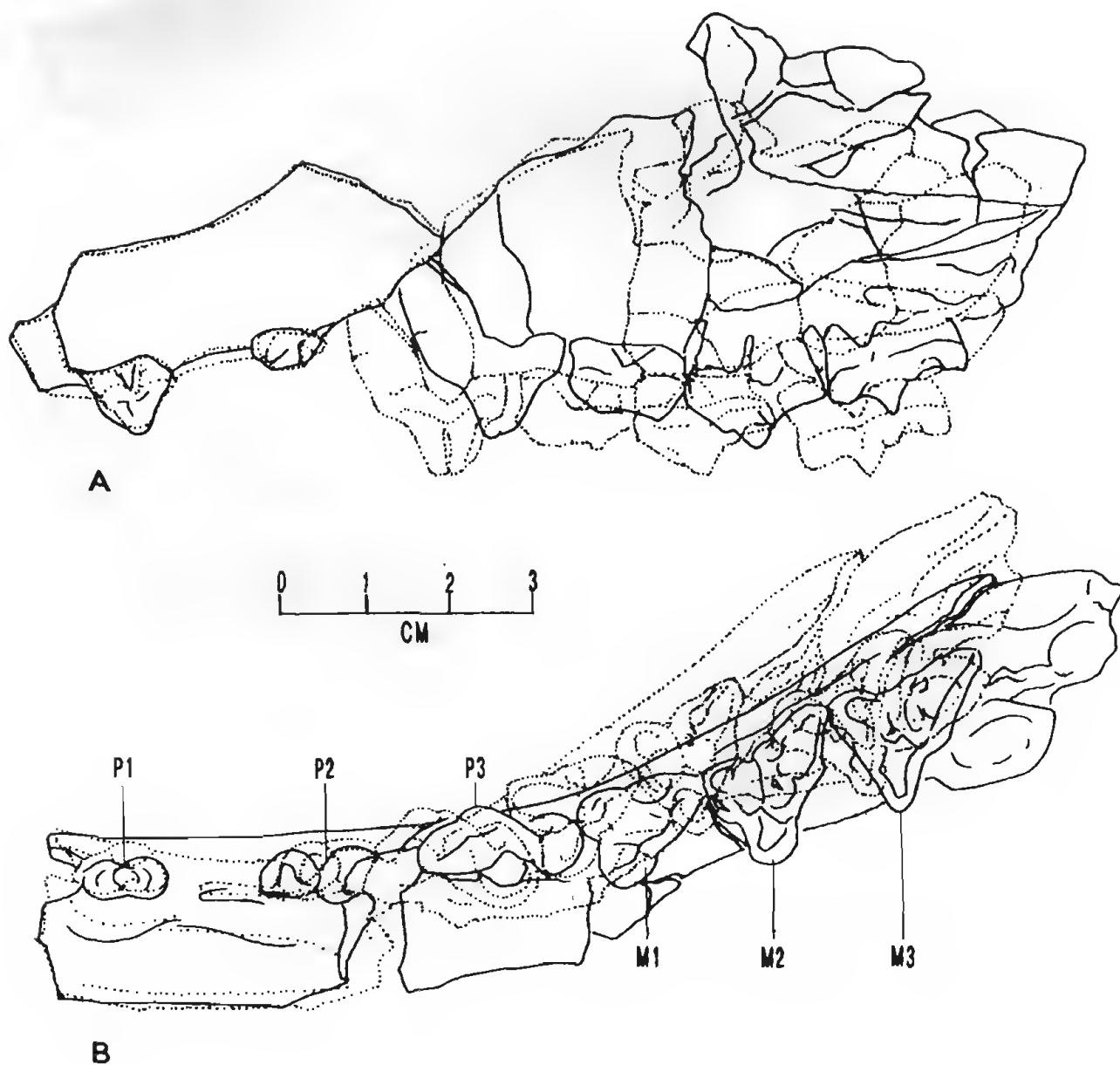


FIGURE 3. Outlines depicting changes made to the initial restoration of the specimen; solid outline represents the new restoration; compare with Fig. 2. **A**, lateral aspect; **B**, palatal aspect. The specimen was taken apart at its primary joints, cleaned of excess Synocryl and glue, and reassembled. The anterior fragment of the rostrum was carefully cleaned revealing a labial expansion representing the anterior alveolus of P^3 . It was glued in place at what is probably the minimum distance from P^3 , as no definite contact could be identified. Removal of additional matrix from a fragment of palate that previously did not seem to fit anywhere on the specimen, revealed the inner lining of the anterior P^3 root and was glued in position. The M^3 was twisted out of alignment with the molar row by about 15° . This region of the specimen, which consisted primarily of impacted matrix and bone fragments was embedded in modelling clay, then softened in acetone and pushed gradually back into its correct position. The area above and internal to the M^3 was then reinforced with dental plaster. These changes resulted in a significant transformation of the occlusal outline of the specimen, which subsequently lost some of its resemblances to *T. potens*.

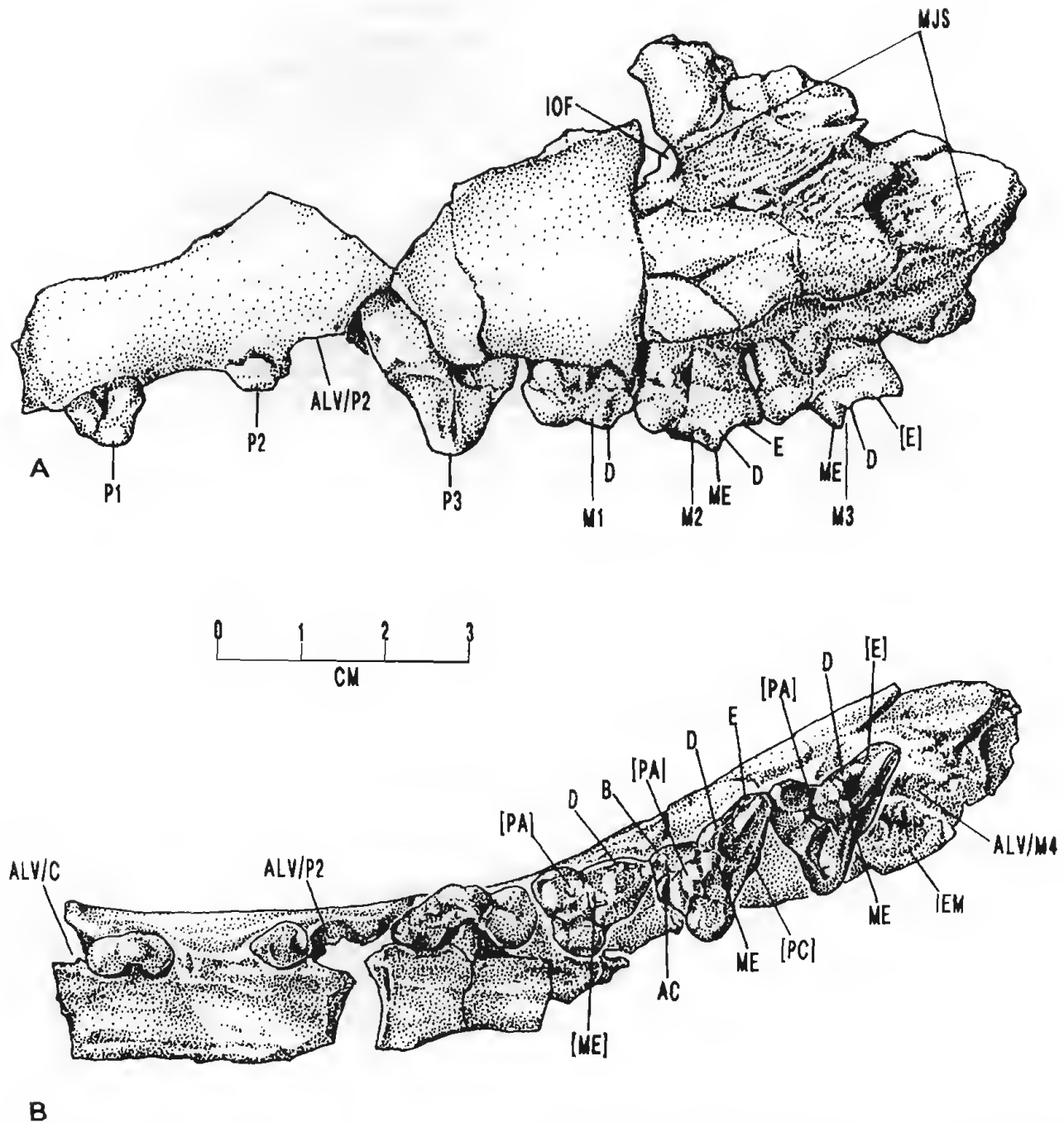


FIGURE 4. Drawing of corrected restoration of *T. megiriani* n. sp. (NTM P9618) left maxilla; A, lateral aspect; B, palatal aspect. Abbreviations: AC, precingulum; ALV/, alveolus; B, stylar cusp B; C, canine; D, stylar cusp D; E, stylar cusp E (brackets [E] indicate doubtful, or if worn, the approximate position of a structure); IEM, interdental embrasure; IOF, infraorbital foramen; M1...3, molars; ME, metacone; MJS, maxillojugal suture; P1...3, premolars; PA, paracone; PC, postcingulum.

T. potens though relatively shorter in proportion to their width than in *T. cynocephalus*. Agrees meristically with *T. cynocephalus* in that M³ is slightly longer than M², differing from *T. potens* and *Nimbacinus dicksoni* in which M² is slightly longer than M³. Length of molars exceeds anterior width from protocone to parastyle; stylar shelf

considerably narrower than in *T. potens*; metastylar spur much larger than parastylar corner on M³, contrasting with *T. potens* in which they are more nearly equal-sized; stylar cusp D present on M¹⁻³ as in *Nimbacinus dicksoni* and probably as in *T. potens*; rudimentary stylar cusp E present on M², absent in *T. potens* and in *T. cynocephalus*

but present on M^{1-2} in *Nimbacinus dicksoni*. Rudimentary anterior cingulum present on M^2 in contrast to *Nimbacinus dicksoni* in which it is well-developed on M^{1-3} , *T. potens* in which it is present on M^{2-3} and *T. macknessi* in which it is present on M^1 , the only upper molar known for that species. A small precingulum is present on M^2 of *T. megiriani*. Ectoflex of M^{2-3} less pronounced than in *T. potens* but greater than in *T. cynocephalus*. Paraconal reduction on M^{1-3} comparable to that of *T. cynocephalus*; protocones on M^{2-3} reduced, similar to *T. cynocephalus*. Infraorbital foramen opens above posterior half of M^2 as in *T. cynocephalus*, unlike *T. potens* in which it opens above M^1 ; maxillojugal suture nearly reaches the margin of infraorbital foramen, approaching the condition in *T. cynocephalus* and in contrast with *Nimbacinus dicksoni* in which it terminates considerably short of the margin of the foramen.

Etymology

It is my privilege to name this species after Dirk Megirian, Geologist, Museums and Art Galleries of the Northern Territory, Darwin, NT; who discovered and meticulously extracted the specimen.

Description

Maxilla

Thylacinus megiriani n. sp. consists of a maxilla that was recovered from nodular calcareous sandstone matrix in about a dozen pieces (Figs 2–4, 7). All but a few small fragments have been assembled into the left side of the animal's snout which includes the base of the zygomatic arch to just below the orbit and the infraorbital foramen and canal, to the posterior margin of the canine alveolus. The full extent of the missing jugal is clearly inscribed by its suture. In palatal aspect the maxilla is shallowly concave on the labial side and the snout was constricted behind P^1 much as in *T. cynocephalus*. The base of the zygomatic arch is convex and marked by a pair of low, irregular crests. The higher one, corresponding to the maxillojugal suture, extends obliquely upwards to immediately behind the opening of the infraorbital foramen.

The infraorbital foramen is a large, approximately 9.0 mm by 10.5 mm opening situated 21.0 mm above the approximate middle of the posterior half of M^2 (Figs 4, 7). Its position in *T. megiriani* is similar to that of *T. cynocephalus* and differs from the more anteriorly situated opening in *T. potens*, above M^1 . Anterior

to the infraorbital foramen, a shallow, oval fossa extends to above P^3 , anterior to which, the lateral margin of the rostrum becomes convex.

A fragment of the maxillary palate extending from P^1 to P^2 is broken at the median suture. A prominent median palatal ridge is apparent, parallel to which runs a deep, 5.0 mm wide palatal groove. The palatal width at between the posterior roots of P^1 would have been about 24.0 mm, approximately 5.0 mm wider than in *T. potens*. The palate is narrower at this point in *T. potens* because the posterior roots of P^1 are angled inwards and are also larger, whereas they are aligned with the median base of the canine anteriorly and the P^2 posteriorly in *T. megiriani* and *T. cynocephalus* (Figs 2–5).

Three additional fragments of the palate can be approximated to adjacent structures medial to P^3 – M^1 (Figs 3, 4) as additional removal of matrix and Synocryl revealed the inner margin of the P^3 alveolus on the largest of the fragments. The premolar diastemata are similar to those of *T. potens* in that the P^1 and the P^2 are widely separated, whereas the diastema between P^2 and P^3 is shorter (Figs 5, 6). In the original restoration of *T. megiriani* (Figs 2, 3) it appeared that the posterior root of P^2 might have overlapped the labial side of the anterior root of P^3 by about 3.0 mm. The specimen is broken at this point and the contacts were not quite congruent, causing the anterior part of the snout to twist out of alignment. This contact was taken apart and cleaned, revealing more of the P^2 alveolus and a straight section of diastema, indicating that a P^2/P^3 diastema of at least 5.0 mm is actually present (Fig. 6). The premolars of *T. megiriani* are large and posteriorly directed, though in proportion to the molars, the first and second premolar crowns and their alveoli are absolutely and relatively smaller than those of *T. potens* (Figs 2–6, Table 1) but the P^3 crown, though not the alveolus, is similar in size to that of *T. potens*. The lengths of the premolar alveoli of *T. megiriani* are as follows: P^1 , 10.5 mm; P^2 , 15.0 mm; P^3 , 18.5 mm. Corresponding measurements of *T. potens* are: P^1 , ~15 mm; P^2 , 17.5 mm; P^3 , 20.5 mm (Fig. 6).

Reconstruction

The reconstructed snout of *T. megiriani* is compared with that of *T. potens* and *T. cynocephalus* in Fig. 5. This reconstruction, based on modifications of the original restoration of the specimen (Fig. 3) indicates that although it is comparable in size and robustness to *T. potens*, its shape is more similar to that of *T. cynocephalus*

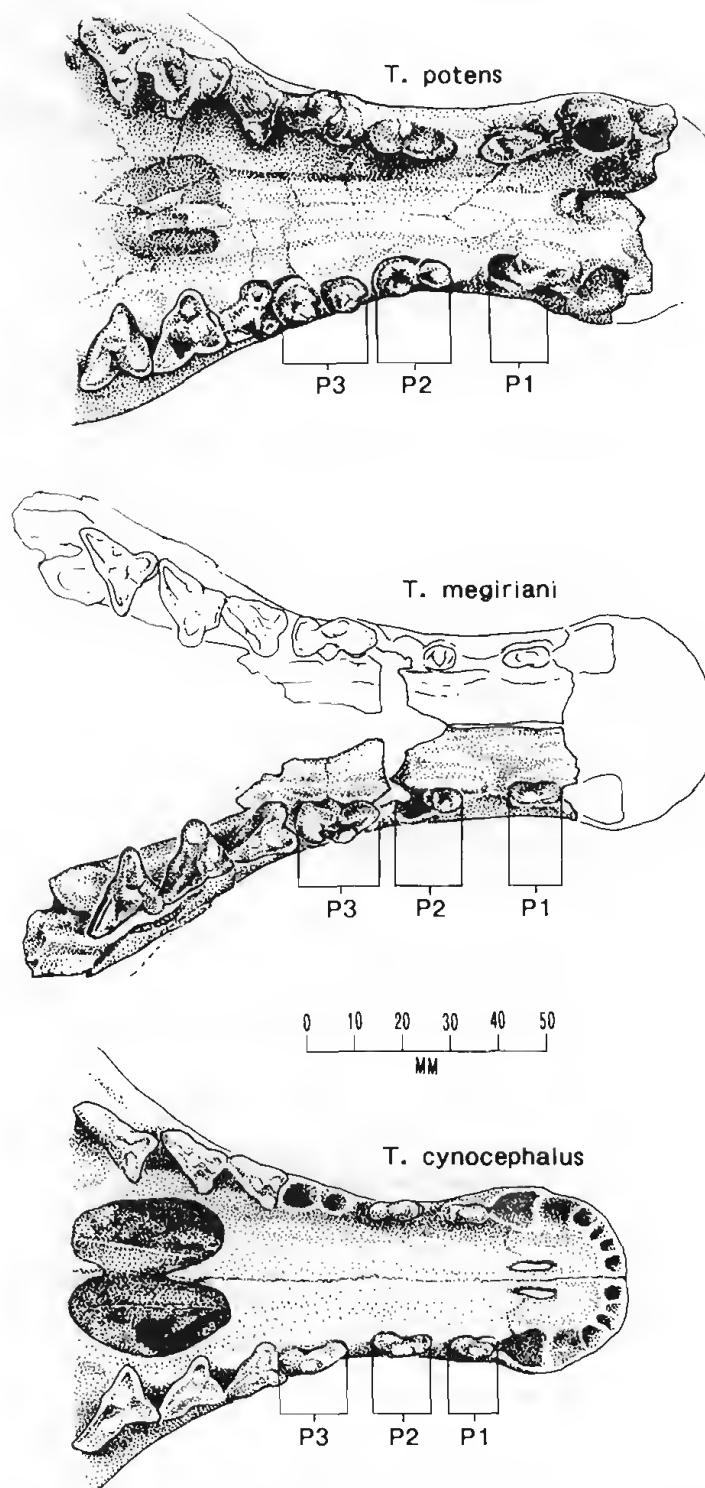


FIGURE 5. Reconstruction of the rostrum of *T. megiriani* n. sp. for comparison with those of *T. potens* and *T. cynocephalus*, drawn to scale. Comparative lengths of the premolar alveoli are indicated by brackets. *T. megiriani* n. sp. is approximately the same size as *T. potens*, both species being considerably larger and more robust than the Recent Tasmanian Wolf, *Thylacinus cynocephalus*. *T. megiriani* differs from *T. potens* in having a wider, less constricted palate at the level of P^1 , in its alignment of the premolars, and in having smaller P^{1-2} alveoli and longer P^3 diastemata, all features shared with *T. cynocephalus*. Distinctive features of the rostrum and palate of *T. potens* include the large size and oblique emplacement of P^1 , distinct narrowing of palate at the level of P^2 , separate rather than confluent P^1 and canine alveoli, emplacement of the P^1 internal to the canine base, the incisive foramina are formed within a deep, oval pit, (apparently absent in *T. megiriani*) and the palatal fenestrae are small.

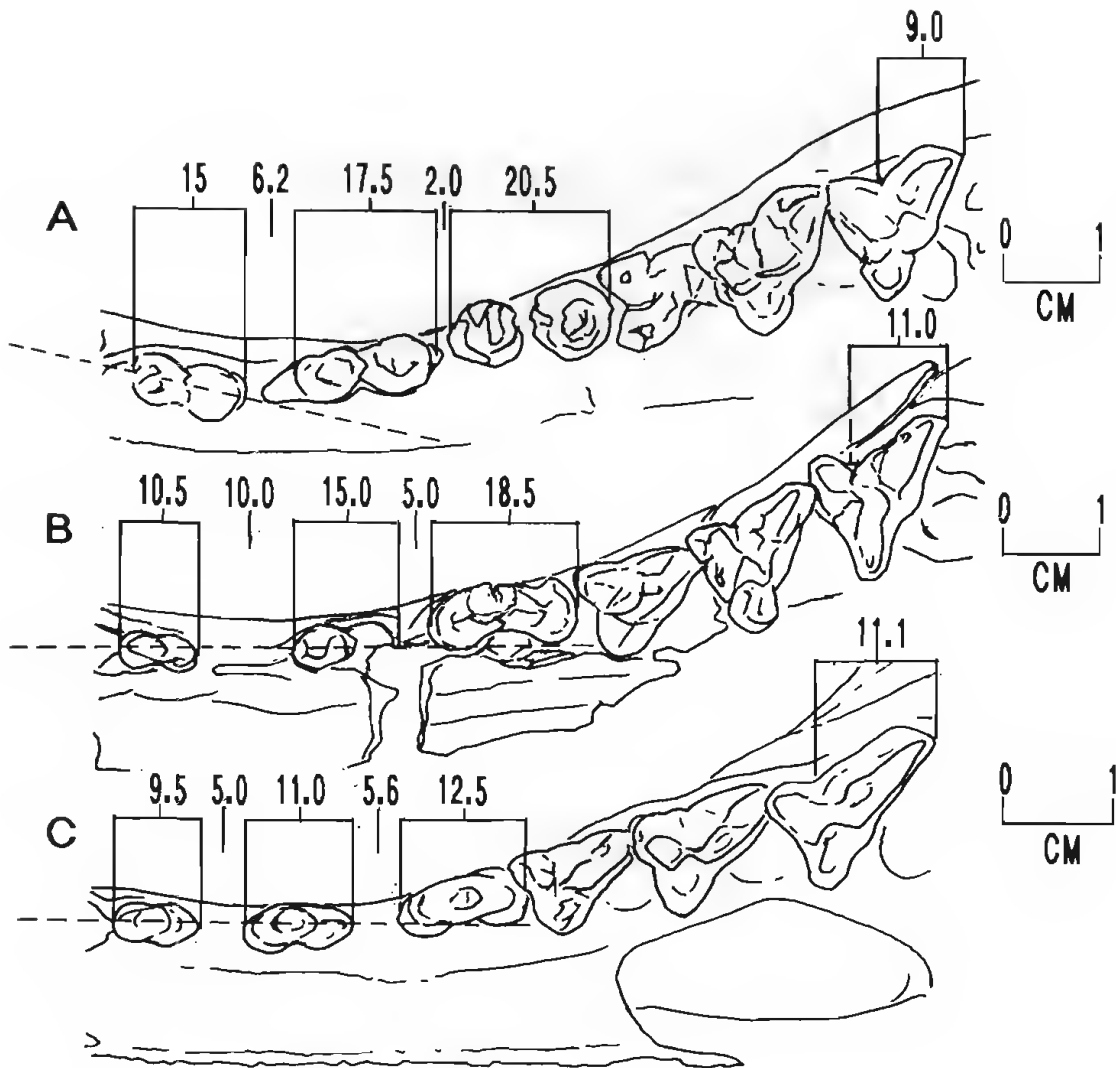


FIGURE 6. Diagram comparing proportional features of the cheek tooth rows of A, *Thylacinus potens*, B, *T. megiriani* n. sp. and C, *Thylacinus cynocephalus*, all drawn to the same length from anterior P^1 to the metastylar tip of M^3 , measurements in millimetres. Refer to seale and actual measurements given above, as brackets show relative rather than sealed dimensions of the alveoli and the length of the metastylar spur from ectoflexus to tip. The P^3 alveolus in *T. potens*, damaged on both sides, is a composite restoration; note the relatively and absolutely longer diastema between P^1 and P^2 in *T. megiriani*, suggesting that the P^2/P^3 diastema was probably slightly longer than restored. The two pieces were glued at this point because no additional surface was available to provide a secure union. Observe that the diastemata in *T. cynocephalus* are approximately equal lengths.

in being more drawn out in the premolar region and in the premolar rows lying essentially parallel to each other, rather than converging at the level of P^2 . As the restored P^2/P^3 diastema is a minimum dimension, the snout of *T. megiriani* may actually have been slightly longer than depicted. The distinctive median pit for the incisive foramina in *T. potens* appears to have been absent in *T. megiriani*. Note also that the P^1 alveolus is confluent with the canine alveolus in *T. cynocephalus* and *T. megiriani*, whereas in *T.*

potens they are separated by a bony ridge. Longitudinal palatal crests define the lateral margins of the palatine fenestrae in *T. potens*. Similar crests in *T. megiriani* are situated further apart, indicating that the palatine fenestrae were probably wider.

Premolars

P^1 is a small two-rooted premolar closely resembling that of *T. cynocephalus*. The crown is 8.5 mm long and 4.5 mm wide. The anterior

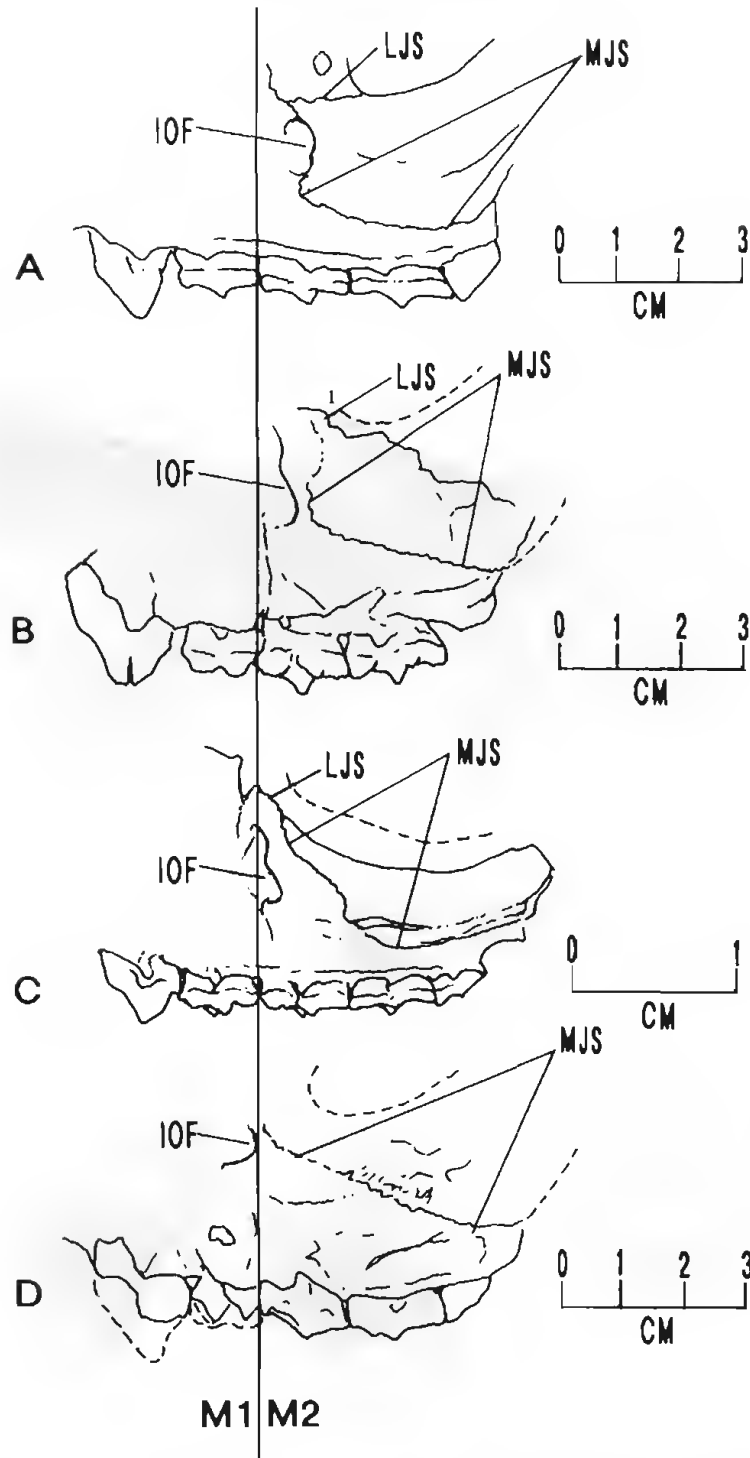


FIGURE 7. Diagram comparing the position of the infraorbital foramen relative to interproximal M^1/M^2 and its relationship to the maxillojugal suture in **A**, *Thylacinus cynocephalus*; **B**, *Thylacinus megiriani* n. sp.; **C**, *Nimbacinus dicksoni* (NTM P907-3) and **D**, *Thylacinus potens*. In this series, the infraorbital foramen in *Thylacinus potens* is positioned more anteriorly than in the other species under consideration. A more anteriorly situated infraorbital foramen is a primitive feature in didelphoids, dasyurids and probably thylacinids. However, the infraorbital foramen in *Nimbacinus* is situated more posteriorly than in *T. potens*, an otherwise much more derived species. Note that the maxillojugal suture lies well posterior to the foramen in *Nimbacinus*, whereas it reaches or nearly reaches the posterior margin of the foramen in *T. potens*, as it does in *T. megiriani* and *T. cynocephalus*. This relationship is a derived feature, suggesting that the forward position of the foramen in *T. potens* is a secondary, rather than a primary condition, indicative of a derived state. Abbreviations: IOF, infraorbital foramen; LJS, lacrimojugal suture; MJS, maxillojugal suture.

margin of the crown commences with an enamel bulge about 3.0 mm above the alveolus. The posterior profile is steeper, longer and slightly concave, terminating in an enamel thickening 1.0 mm above the alveolus (Figs 2–4, Table 1)

P² is represented by its anterior root and posterior alveolus. Its alveolus is about 15.0 mm

long, 2.5 mm shorter than that of *T. potens*. The posterior alveolus is slightly larger in diameter than the anterior one.

P³ is considerably the largest premolar. The length of the crown at the base of the enamel is about 16.5 mm. The circular, heavily worn postcrobasal cuspule is 8.5 mm transversely,

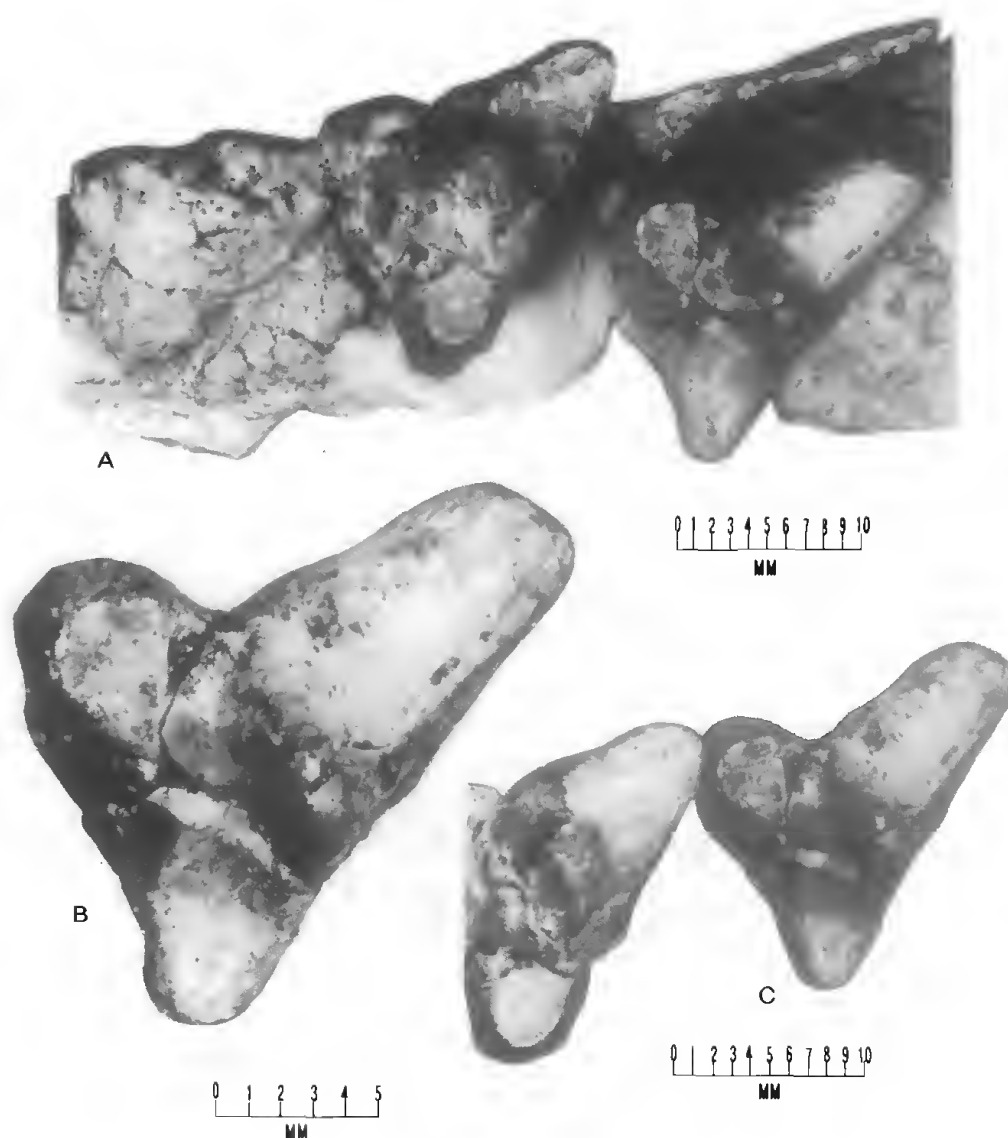


FIGURE 8. Photographs of the left M¹⁻³ of *Thylacinus megiriani* n. sp.; A, M¹⁻³, taken before correction of the position of M³ on the specimen; B, enlargement of M³ showing stylar cusp D and possible aberrant stylar cusp E, which may actually be a peculiar wear artifact; C, paste-up showing the approximately correct alignment of the M² metastyle with the parastylar corner of M³. Because of its dislocation, the occlusal surface of M³ is tilted more lingually than those of M¹⁻², revealing the entire buccal side of the crown and resulting in the misleading impression that the metacone is situated more posterolingually than it actually is. Note the faint, postcingulum-like structure on M¹, the small precingulum on M² and absence of same on M³; The remnant stylar cusp E on M² is indistinct in A, but is faintly visible in C.

while the width across the anterior enamelled part of the crown immediately above the posterobasal cuspule is 7.0 mm. The crown is heavily worn on the anterior and posterior surfaces where distinct wear facets result in a steep, slightly biconcave profile.

Molars.

M¹ is heavily worn (Figs 2, 4, 8A, 9C). Both the paracone and metacone have been ground flush with the styler shelf. The remnant base of the paracone indicates that it was probably reduced relative to the metacone. A remnant V-shaped 'wall' of vertical facets above the premetacrista and centrocrista are faintly visible on the specimen. Styler cusp D, situated immediately posterior to the labial cleft, is the highest relief on the worn occlusal surface. Styler cusp E is not apparent. The protocone is round and slightly constricted near its base. A faint cingulum-like crest extends from a low bulge located about mid-way between the base of the protocone and the metastylar tip, though its exact form and extent is obscured by a layer of calcite. The length of the tooth along the styler crest is 14.7 mm. Its transverse width from the protocone to the parastyle is 12.3 mm and its posterior width from protocone to metastyle is 16.0 mm. The M¹ of *T. megiriani* is similar, but relatively longer than the equivalent tooth in *T. potens* (Fig. 9B) differing from that of *N. dicksoni* (Muirhead & Archer 1990) in its reduced styler shelf, reduced paracone and absence of an anterior cingulum (Fig. 9A) and from that of *T. macknessi* (Muirhead 1992) in its retention of a distinct styler shelf remnant with a large styler cusp D, in the reduction of the paracone, in the absence of an anterior cingulum, and in having a steep facet or 'wall' above the paracone and metacone bases (Fig. 9D).

M² is considerably larger than M¹ and broader transversely, though slightly shorter across the styler wings than M³ (Figs 2, 4, 8A, C, 9C; Table 1). Its length from parastyle to metastyle is 16.8 mm. Its anterior transverse dimension from protocone to parastyle is 15.0 mm and its posterior transverse dimension from protocone to metastyle is 19.5 mm. The parastylar corner is small compared to the metastylar corner. The smaller, lower and narrower paracone is cleanly divided from the metacone by a mesial continuation of the labial cleft. Approximately 3.0 mm distal to the labial cleft and 2.0 mm labial of the metacone is a prominent styler cusp D. It is connected to the metacone by a short crest. Separated by a shallow

labial groove from styler cusp D is a second, much smaller enamel expansion situated about 3.0 mm anterior the metastyle, which appears to represent a remnant styler cusp E. Although not prominent, the tiny cusp has a small wear facet and a labial bulge on the styler shelf is evident. The anterolingual surface between the protocone and parastyle is distinctly convex and emarginated by a short, though strong precingulum. The protocone is smaller than on M¹ and is more U-shaped than rounded. Remnants of the pre- and post-protocristae extend from either side of the apex of the protocone to the bases of the paracone and metacone respectively. A small, but distinct lobe is situated immediately above the dentine-enamel junction, approximately midway between the metastyle and the protocone. In overall shape, the M² of *T. megiriani* is structurally intermediate between *Nimbacinus dicksoni* and *T. potens*, but differs from both in having a much reduced parastylar wing, reduced paracone and relatively reduced height of the styler shelf. There is no indication of styler cusp E on *T. potens*, but the cusp is well-developed, though small, in *Nimbacinus dicksoni*.

M³ is slightly longer and more slender across the metastyle and protocone than M². The anterolingual and posterolingual emarginations are reduced and the precingulum is rudimentary (Figs 2, 4, 8B, C, 9C; Table 1). The parastylar spur is smaller in proportion to its metastylar component than in the previous molar, though the ectoflex is more pronounced on M³ than on M². The length of the crown from parastyle to metastyle is 17.4 mm. Its anterior transverse dimension is 16.1 mm and its posterior transverse dimension is 20.3 mm. Though heavily worn, it is apparent that the paracone was originally low, narrow and much smaller than the metacone, which in turn, is high, transversely elongated and anteroposteriorly narrow. As in *Thylacinus cynocephalus*, the preparacrista is short and the internal angle formed by the preparacrista and postmetacrista is more obtuse than in *T. potens*. Prominent pre- and postprotocristae meet at the apex of the narrow, V-shaped protocone. Both crests extend to near the cusps of the paracone and metacone accentuating a furrow-like occlusal fossa between them. Styler cusp D is situated ~3.0 mm posterior to the labial cleft in the same position relative to the posterolabial base of the metacone as in M². It is connected to the metacone by a low crest. A possible rudiment of styler cusp E is situated about 4.0 mm anterior to the metastyle. Though small, it is more obvious than

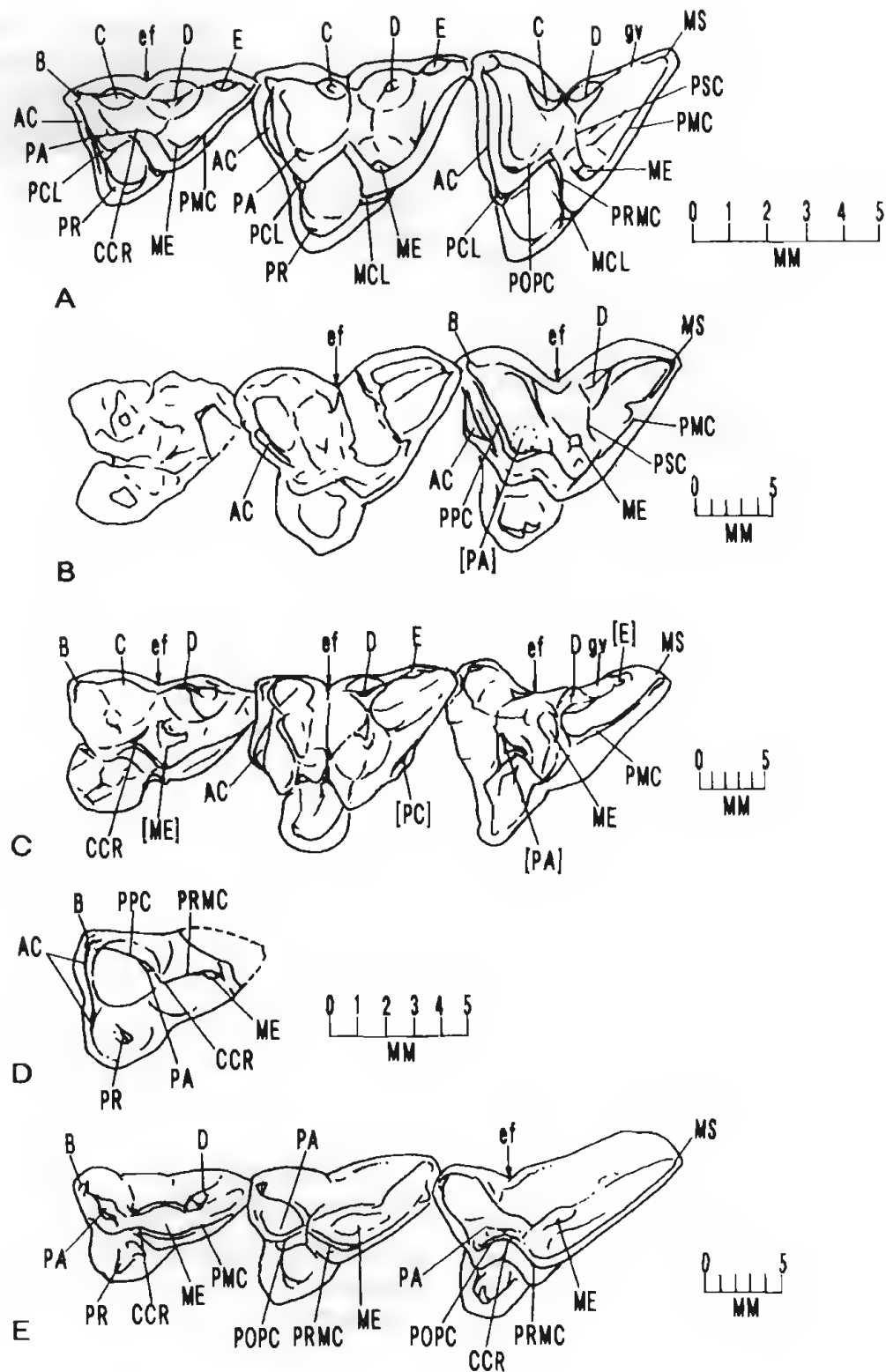


FIGURE 9. Comparison of M^{1-3} of *T. megiriani* n. sp. with thylacinid species: A, *Nimbacinus dicksoni* (NTM P907-3); B, *Thylacinus potens*; C, *Thylacinus megiriani*; D, *Thylacinus macknessi* (M^1 reversed for comparison); E, *Thylacinus cynocephalus*. Abbreviations: AC, precingulum; B, stylar cusp B; C, stylar cusp C; CCR, centrocrista; D, stylar cusp D; E, stylar cusp E; ef, ectoflexus; gv, natural or wear groove in stylar shelf; MCL, metaconule; ME, metacone; MS, tip of metastyle; PA, paracone; PC, postcingulum; PCL, paraconule; PMC, postmetacrista; POPC, postparacrista; PR, protocone; PRMC, premetacrista; PSC, crest connecting metacone and stylar cusp D.

TABLE 1. Measurements of cheek teeth of *Thylacinus megiriani* compared with those of *T. potens* and *T. cynocephalus*.

		<i>T. megiriani</i> NTM P9618	<i>T. potens</i> CPC6746	<i>T. potens</i> UCMP 66971	<i>T. cynocephalus</i> sample means (Woodburne 1967)
P ¹	L	8.5	—	—	6.2
	W	4.5	—	—	3.3
P ²	L	<12.0	12.4	—	8.3
	W	<5.0	5.5	—	3.8
P ³	L	16.5	16.0	—	10.6
	W	8.5	8.8	—	5.0
M ¹	L	14.7	12.0	—	10.9
	W ₁	12.3	12.8	—	11.5
	W ₂	16.0	13.5	—	11.5
M ²	L	16.8	15.7	—	13.2
	W ₁	15.0	13.9	—	10.0
	W ₂	19.5	17.5	—	15.0
M ³	L	17.4	15.2	14.6	15.1
	W ₁	16.1	15.9	14.7	12.0
	W ₂	20.3	19.0	17.5	17.8

the structure in the equivalent position on M². It consists of a nearly circular raised enamel ridge with an oval wear facet or pit in the centre (Fig. 8 B, C). After long deliberation of the structure under the microscope, I have concluded that it could represent a freakish wear pattern, but that it also indicates that thicker, more obdurate enamel is located where stylar cusp E would be anticipated. The enamel on the molars of this specimen is uniformly quite thick and it may be the case that some of these small structures, including the postcingulum-like crests on M¹⁻² might be the result of an exceptionally active enamel organ. A ~3.0 mm wide attrition furrow between stylar cusp D and the equivocal cusp E extends vertically some 4.0 mm up the labial side of the stylar crest.

Meristic gradients of the molars are as follows: metastyle to parastyle length, M¹<M²<M³; ectoflex, M¹<M²<M³; Protocone base diameter, M¹>M²>M³; Paracone, M¹>M²>M³; Metacone diameter, M¹?M²>M³; Metacone height, M¹?M²<M³; Parastyle length, M¹>M²>M³; Metastyle length, M¹<M²<M³; Precingulum, M¹ nil M² present M³ nil; Stylar cusp D, M¹>M²>M³; Stylar cusp E, ? M¹, weakly expressed on M², ? M³; ?Postcingulum length, M¹>M² nil on M³.

DISCUSSION

The similarity in size and robusticity of *T. megiriani* to *T. potens* contributed to some of the errors in the initial restoration and interpretation of the fragmentary specimen. The new restoration of the fossil indicates that *T. megiriani* was a long-snouted species, proportionally more similar to *T. cynocephalus* than to *T. potens*. The length of the diastema between P² and P³ is a minimum estimation, as no definite contact between the two fragments of the snout could be identified. The posterior margin of the fragment containing P² shows a definite lateral expansion for the anterior root of P³, but the actual alveolar margin and internal lining of compact bone is absent (Fig. 3). Consequently, *Thylacinus potens* appears to have undergone proportional changes in the rostrum, possibly a forward adjustment of the zygomatic root to shift the line of action of the masseter muscle more anteriorly. Apparently related to differences in the proportions of the snout is the position of the infraorbital foramen in *T. potens*. In that species the foramen is situated more anteriorly than in *Nimbacinus dicksoni*, yet the maxillojugal suture terminates close to the margin of the foramen as in *T. megiriani* and *T.*

cynocephalus (Fig. 7). In *Nimbacinus*, the maxillojugal suture terminates a considerable distance posterior to the foramen. This particular combination of characters suggests that the condition in *T. potens* is secondary, or specialised rather than primitive, having occurred in conjunction with telescoping of the base of the rostrum.

Another specialisation in *T. potens*, now apparent, is the obliquity and rather large size of the P^1 alveolus, which is part of an overall proportional shift of the cheek tooth row in relation to the rostrum. In *Nimbacinus dicksoni*, the P^1 is relatively small and lies in direct line with P^{2-3} as in *T. megiriani* and *T. cynocephalus* indicating that the condition is derived. However, the position of the P^3 relative to the canine in *T. potens* is like that of *Nimbacinus dicksoni* in lying medial to the canine and in being separated from the canine alveolus by a small bony crest. These latter features are probably symplesiomorphic, whereas the relationship of the P^3 to the canine alveoli in *T. megiriani* and *T. cynocephalus* is probably synapomorphic.

Comparison of the molar morphology among *T. potens*, *T. megiriani* and *Nimbacinus dicksoni* shows a similar mixture of plesiomorphic and derived character states (Fig. 9A–E). In some aspects, such as molar shape and development of the stylar shelf, *T. megiriani* resembles *Nimbacinus dicksoni* more than it does *T. potens*. In *T. potens* the stylar shelf is high and wide, yet appears to show more reduction of the stylar cusps than *T. megiriani* and certainly more reduction than in *Nimbacinus* in which the stylar cusps D and E are well-developed on M^{1-2} , though cusp E is absent on M^3 . *T. potens* shows a much greater development of the ectoflex on M^{2-3} than either *T. megiriani* or *Nimbacinus dicksoni*. These appear to be derived characters of the dentition of *T. potens*, which however, also shows some plesiomorphic states relative to *T. megiriani* and *T. cynocephalus* in retaining a well-developed precingulum on M^{2-3} , in retaining large protocone bases and in the length of M^2 exceeding the length of M^3 . *T. megiriani* is derived relative to *Nimbacinus dicksoni* and *T. potens* in M^3 being slightly longer than M^2 , in having more slender and proportionally longer metastylar spurs, in having reduced protocones and more reduced paracones, in the loss of the precingulum on M^3 and in having a more obtuse angle between the preparacrista and the postmetacrista. These features of *T. megiriani* trend towards the more derived states found in the molars in *T.*

cynocephalus. However, *T. megiriani* is plesiomorphic relative to *T. potens* in retaining a vestige of stylar cusp E on M^2 and if the structure on M^3 represents a stylar cusp, it is autapomorphic (?reversal, eg. Marshall *et al.* 1994) among all known thylacinids in that respect.

The heavily worn condition of M^1 of *Thylacinus megiriani* renders comparison with the unworn equivalent of *T. macknessi* (Muirhead 1992) somewhat less informative. *Thylacinus macknessi* possess a well-developed anterior cingulum, which is clearly absent in *T. megiriani*. In *T. macknessi* the pre- and postprotocristae do not ascend the paracone and metacone bases to form acute crests as they do in all other thylacines including the M^1 of *T. megiriani*. The stylar shelf is well-developed on the M^1 of *T. megiriani* and much reduced in *T. macknessi*. The molar is broken in a critical position in relation to the position of stylar cusp D. In *T. megiriani*, stylar cusp D is very large and lies immediately adjacent to the metacone. This suggests that the cusp may have been reduced in *T. macknessi*. This comparison agrees in all aspects with Muirhead's (1992) observations that *T. macknessi* is more derived in the development of these features than *T. cynocephalus*, yet plesiomorphic in the retention of the anterior cingulum and autapomorphic in its extension from stylar cusp B to the base of the protocone.

Stylar cusp homologies among thylacines were more ambiguous when *T. potens* was the only fossil form of any antiquity known (Archer 1982). The expression of the cusps in *Nimbacinus dicksoni* is now well-documented, and accords with other members of the family Thylacinidae (Muirhead & Archer 1990). In *Nimbacinus dicksoni*, stylar cusps B, D and E are present on M^{1-2} and stylar cusp D is present on M^3 whereas cusp E is absent from that tooth. In *T. potens*, stylar cusp D is definitely present on M^3 and almost certainly was present on M^{1-2} , though the crowns are damaged in the region that the cusps are usually situated. There is no sign of stylar cusp E on M^{2-3} in that species. In *T. megiriani*, stylar cusp D is well-developed on M^{1-3} whereas stylar cusp E is rudimentary on M^2 . I am disinclined to attribute any phylogenetic significance to the cusp-like structure in the position of stylar cusp E on the M^3 of *T. megiriani*, although its putative existence is duly noted should future finds serve to either verify or negate its presence.

In *T. cynocephalus*, stylar cusps are absent on M^{2-3} in conjunction with the reduction of the stylar shelf. A small stylar cusp occupying the usual

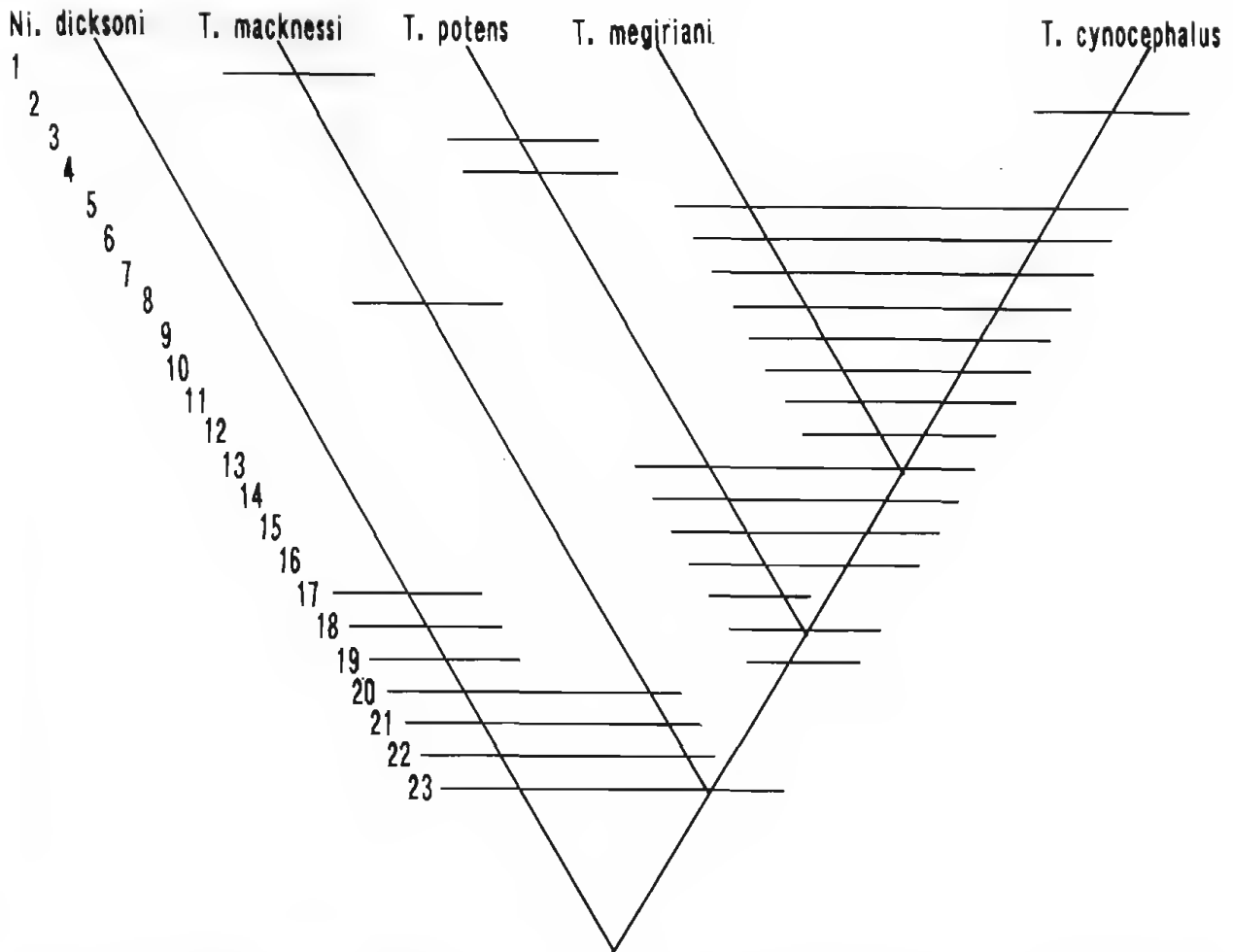


FIGURE 10. Character distribution in species of Thylacinidae. 1–16 are apomorphic, 17–23 are plesiomorphic: 1, loss of ‘wall’ below postparacrista and premetacrista; 2, transverse narrowing of molars and loss of stylar cusp D on M^{2-3} ; 3, widened, elevated stylar crest, suppression of stylar cusp E at least on M^2 ; 4, increased ectoflex; 5, lengthened premolar diastemata; 6, confluent P^1 –C diastema; 7, elongation of metastyle, reduced parastyle, obtuse angle between preparacrista and postmetacrista, M^3 longer than M^2 ; 8, reduced stylar shelf; 9, reduced protocone; 10, loss of precingulum and increased concavity of anterior margin of M^3 ; 11, reduced ectoflexus; 12, posterior position of infraorbital foramen above middle of M^2 ; 13, reduced paracone; 14, loss of precingulum on M^1 ; 15, forward extension of maxillojugal suture to posterior margin of infraorbital foramen; 16, large body size; 17, (plesiomorphic) absence of diastema between P^2/P^3 ; (plesiomorphic) notched precingulum on M^2 – M^3 ; 19, (plesiomorphic) P^1 situated lingual to canine; 20, (plesiomorphic) retention of precingulum on M^1 ; (plesiomorphic) 21, large paracone; 22, (plesiomorphic) metaconid on M^3 ; 23 (plesiomorphic) small body size.

topological position of stylar cusp E is present on M^1 . This cusp was initially identified by Archer (1982) as stylar cusp E. Subsequently, Muirhead and Archer (1990) identified the cusp as stylar cusp D that had become reduced and migrated posteriorly in conjunction with the elongation of the metastyle. The predisposition of the stylar cusps in *T. megiriani* supports the latter conclusion, in that if stylar cusp E was present, it was already extremely reduced relative to stylar cusp D. Moreover, there is no satisfactory

explanation of the fate of stylar cusp D had cusp E been retained, as its amalgamation with the metacone, analogous to *Sarcophilus* (Crabb 1982) appears to have been highly unlikely (Stephen Wroe, pers. com.).

Phylogenetic position of *T. megiriani*

The character evaluations employed here are based on those of Muirhead and Archer (1990). As the new species exhibits additional structures,

the character polarities pertaining to those structures are based on the observations made in the discussion. An hypothesis of the phylogenesis of *T. megiriani* is drawn from the following postulations (Fig. 10):

Thylacinus cynocephalus–*T. megiriani* synapomorphies: lengthened premolar diastemata, confluent canine– P^1 alveoli, posteriorly situated infraorbital foramen (in line with middle of posterior half of M^2), elongation and narrowing of the metastyle of M^3 (including M^3 longer than M^2 , reduced width of parastyle, obtuseness of angle of postmetacrista and premetacrista and reduction of height of stylar shelf), greatly reduced paracone particularly on M^{2-3} , reduction of diameter of protocone base, loss of precingulum and concave profile of anterior surface of M^3 , reduction of ectoflexus on M^{2-3} .

Thylacinus potens–*T. megiriani*–*T. cynocephalus* synapomorphies: loss of precingulum on M^1 , forward extension of maxillojugal suture to margin of infraorbital foramen, possibly large size.

Thylacinus potens–*Nimbacinus dicksoni* symplesiomorphies: absence of diastema between P^2 and P^3 , presence of precingulum on M^{2-3} , P^1 situated lingual side of canine.

Thylacinus macknessi–*Nimbacinus dicksoni* symplesiomorphies: retention of anterior cingulum on M^1 , large (unreduced) paracone, possibly small size, remnant metaconid on M^3 .

Thylacinus megiriani–*Nimbacinus dicksoni* symplesiomorphy: expression of stylar cusp E on M^2 .

Thylacinus megiriani apomorphies: possible expression of stylar cusp E on M^3 (reversal?), possible expression of anterobasal cuspule or small postcingulum on M^{1-2} (?neomorphic).

Thylacinus potens apomorphies: extreme development of labial emargination of molars, stronger ectoflexus on M^{2-3} , forward position of infraorbital foramen, obliquity and large size of P^1 , enlarged trigonid and/or reduced talonid in lowers.

Thylacinus macknessi apomorphies: extreme reduction of stylar shelf, absence of crests ascending lingual bases of paracone and metacone, postparacrista and premetacrista connect low in the crown basin consequently the lingual wall below the paracone and metacone is absent.

Thylacinus cynocephalus apomorphies:

extreme elongation of metastyle on all molars, extreme reduction of stylar shelf, loss of stylar cusp D on M^{2-3} .

Probably because there are so few species and relatively few characters due to the fragmentary nature of the fossils, the resulting phylogeny seems to be fairly straight-forward (Fig. 11). Among the species considered, *Nimbacinus dicksoni* is by far the least derived form. In contrast, *T. macknessi*, while retaining more plesiomorphic features than any of the remaining species, is simultaneously more specialised than *T. cynocephalus*. It is therefore the least likely candidate for ancestry of any of the three later species (*T. potens*, *T. megiriani* and *T. cynocephalus*). *T. potens* is also highly derived in its extreme thickening of the labial emargination of the molars, deep ectoflex, relatively narrow talonid and possibly in some degree of rostrofacial proportional sliding. This species shows subtle modification of the relative proportions of the snout that are probably secondary because the forward extent of the maxillojugal suture relative to the infraorbital foramen appears to be synapomorphic with *T. megiriani* and *T. cynocephalus*. In several respects, *T. megiriani* is the least derived of the large species in retaining a rudimentary stylar cusp E on M^2 , in retaining large stylar cusps D on M^{1-3} and in retaining a general proportional similarity in its molars to those of *Nimbacinus dicksoni*. However, other characters of *T. megiriani* show closer resemblances to those of *T. cynocephalus* than observed in any of the other species.

In general appearance, the differences between *T. megiriani* and *T. potens* are quite subtle. Its large size and robustness, relatively small, broad molars, large P^3 , presence of stylar cusp D and deep maxilla all bear a close resemblance to *T. potens*, to the extent that when I first saw the specimen in the field, I thought it might represent an extreme individual variation of the latter species. This resemblance biased my initial restoration of the specimen, although in spite of this, its detailed differences considerably outweighed the introduced and genuine similarities. It is an important feature of the specimen that while the state of many of its characters show an unambiguous trend towards *T. cynocephalus*, it is probably further removed structurally from the modern species than it is from *T. potens*. A reasonable stage of evolution estimation for the time of separation of *T. potens* and the lineal ancestor of *T. megiriani* would be in the later part of the mid-Miocene.

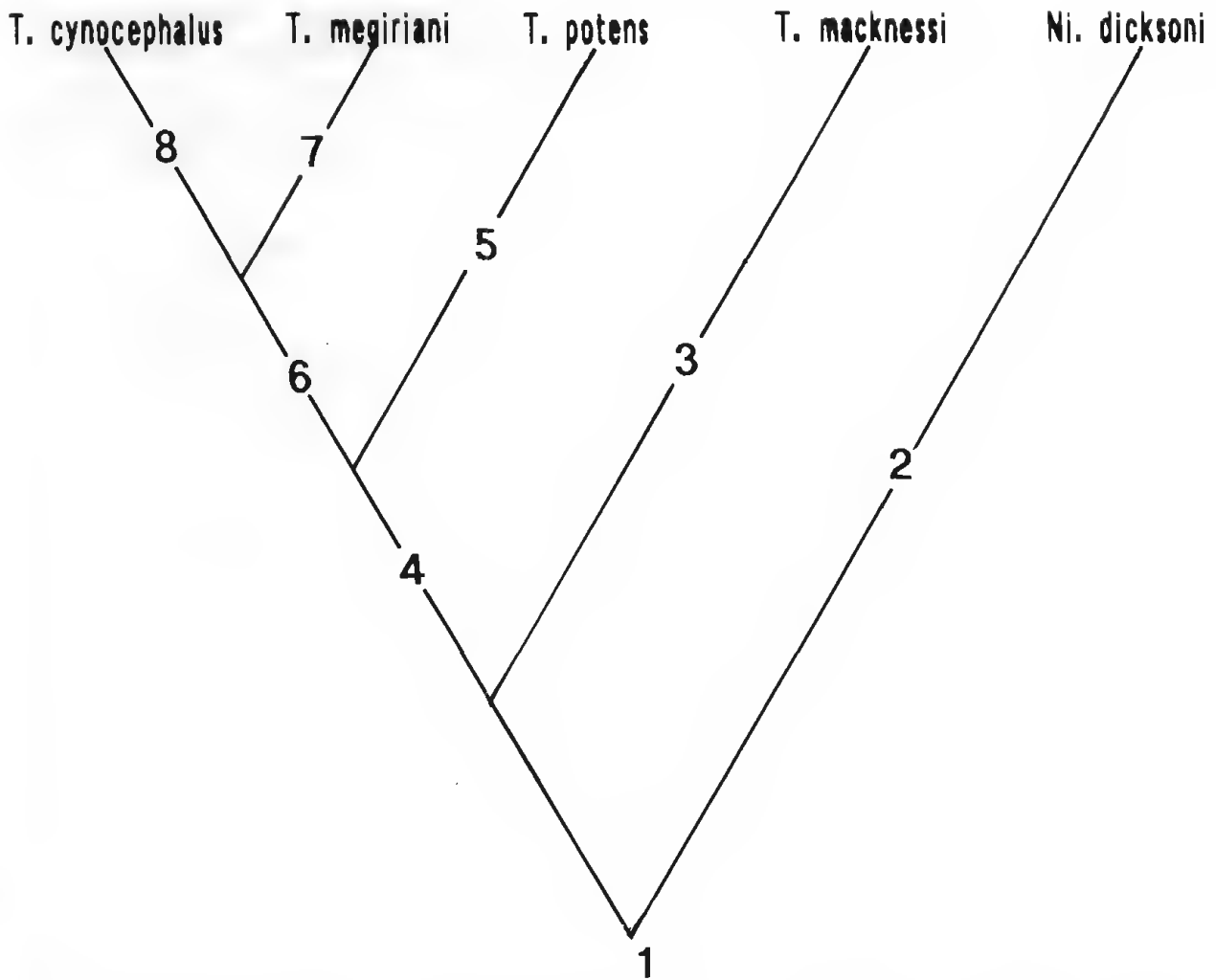


FIGURE 11. Subjective dendrogram depicting hypothesis of phylogenetic relationships among thylacinid species; 1, loss of styler cusp E on M^3 , loss of high postcingulum M^{1-3} , plesiomorphic states of large paracone and small size; 2, more posterior position of infraorbital foramen; 3, reduced styler shelf, loss of 'wall' above postparacrista, centrocrista and premetacrista, extended precingulum M^1 ; 4, loss of precingulum on M^1 , forward extension of maxillojugal suture to margin of infraorbital foramen, large size, reduction of styler cusp E on ?all molars; 5, widened, elevated labial emargination of molars, increased ectoflex on M^{2-3} , loss styler cusp E on at least M^2 ; 6, increased length premolar diastemata, reduced styler shelf, reduced parastyle and paracone, lengthened metastyle, reduced ectoflex, more posteriorly situated infraorbital foramen; 7, possible neomorphic faint, low postcingulum on M^{1-2} , possible styler cusp E on M^3 ; 8, increased reduction of styler shelf, increased elongation of metastyle, styler cusp D confined to M^1 , reduced ectoflex.

Palaeobiology and biochronology

The Ongeva Local Fauna shows a distinct faunal change from the underlying Alcoota LF. A zygomaturine, close to, if not synonymous with *Zygomaturus gilli* is the dominant large herbivore, apparently replacing *Plaisiodon centralis* which it resembles somewhat in size and general morphology. A species of the crocodile *Quinkana* is relatively common, whereas the dominant Alcoota crocodilian, *Baru*, is absent. Though the sample is too small to be definitive, it would

appear that *T. megiriani* had replaced the Alcoota LF thylacinid species, *T. potens* by Ongeva times. A new small ratite bird, possibly a dromornithid, is also present in the Ongeva LF (Megirian, Murray & Wells 1996).

Continuity with the Alcoota LF is indicated by the presence of *Kolopsis torus* Woodburne 1967, *Dorcopsoides* sp., *Dromornis* sp. cf. *D. stirtoni* and *Ilbandornis* sp. The Ongeva *K. torus* appears to be little changed from the Alcoota population, suggesting a fairly short interval between the two local faunas. Because the depositional

circumstances of the two faunas differ, it is not entirely clear as to whether the samples represent distinct communities within a basically stable environment or are a reflection of more general, possibly fairly rapid changes in the biotic attributes of the region.

Thylacinus potens is a highly specialised thylacinid showing as least as much, if not more, derivation in its molar morphology from *Nimbacinus dicksoni* than *T. megiriani*. The increased width of the styler area and relative widening of the trigonids and narrowing of the talonids of the lower molars, combined with its robust skeletal attributes, indicate that *T. potens* was capable of shearing and crushing highly resistant tissues, and may have been somewhat hyena- or *Osteoborus*-like in its habits. *T. megiriani* shows an incipient trend towards the extreme carnassialisation that distinguishes *T. cynocephalus*; consequently it may have been more actively predacious in its habits than *T. potens*. It is likely that the two species would have considerable overlap in their habitat preference and behaviour. Given their close similarities and large size, it seems improbable that they would have occurred sympatrically. Such large predatory species usually have a considerable range, and it is therefore a more plausible speculation that *T. megiriani* represents a successional replacement of *T. potens* rather than an addition to the previously existing fauna.

CONCLUSIONS

As in *T. potens*, the new species has a large P³, retains styler cusp D and has transversely wide molars. *T. megiriani* differs from *T. potens* in many of the features that also serve to distinguish the latter from *T. cynocephalus*. These include reduced ectoflex of M²⁻³ and styler shelf on M³, increase in the length relative to width of M³, narrow protocones, reduction of P¹⁻² relative to the molars, alignment of the premolar row and infraorbital foramen opening above posterior M². *T. megiriani* shows no definite structural features that would preclude it from ancestry of *T. cynocephalus* and shows a number of synapomorphous features including reduced paracone and lengthened postmetacrista. *T. megiriani* is less specialised within the morphological extremes of the large size and powerful shearing/crushing dentition of *T. potens*

and the small-sized, extreme shearing modifications of *T. macknessi*. The addition of this specimen to the small existing collection of fossil thylacines seems to help clarify and simplify our current understanding of the phylogeny of the group.

Thylacinus macknessi indicates that a highly derived shearing complex had evolved in the early to mid Miocene among thylacinids, but did not lead to the development of the Recent thylacine species, *T. cynocephalus*, which appears to have originated in the late Pliocene. It is likely therefore that extreme carnassialisation in the larger thylacinid species took place in the late Cainozoic, perhaps in response to the radiation of macropodine species that commenced in the early to mid Pliocene (Flannery 1989). A tempting speculation, based on the circumstantial evidence for periodic drought in Alcoota times (Murray & Megirian 1992) is that there may have been an abundance of carrion over a sufficient duration to have selected for a large mammalian scavenging species. Following subsequent climatic amelioration in the terminal Miocene, the hyena-like *T. potens* was out-competed by the more predacious *T. megiriani*. The subsequent loss of *Thylacinus potens* as a possible scavenging predator may have left the somewhat less productive scavenging niche open, recruiting a smaller species; namely, the ancestor of the living Tasmanian Devil, *Sarcophilus harrisi*.

ACKNOWLEDGMENTS

I am indebted to Jeannette Muirhead and Alex Baynes for their useful comments on the first draft of this paper. Their observations led to the correction of a number of important details relating to the original restoration of the specimen and several key morphological features of which I was unaware were generously and courteously pointed out to me. I thank Dirk Megirian for his outstanding contribution to all aspects of the excavation, interpretation and documentation of the Alcoota/Ongeva Locality and, of course, for giving me the opportunity to describe and name this interesting species after him. I am very grateful to Ian Archibald, the NT Museum's Preparator/Taxidermist who photographed and printed the bromides under difficult circumstances. I also thank Rod Wells and the Flinders University students who participate in the Alcoota excavations annually. The field work at Alcoota is partially supported by an NT Heritage Grant.

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VOLUME 30 PART 1

JULY 1997

ISSN 0376-2750

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RECORDS OF THE SOUTH AUSTRALIAN MUSEUM

VOLUME 30 PART 2
JANUARY 1998

A NEW SPECIES OF MULTIPHASED CORBULIPORA MACGILLIVRAY, 1895 (BRYOZOA: CRIBRIOMORPHA) FROM SOUTHWESTERN AUSTRALIA.

P. E. BOCK & P. L. COOK

Summary

A new Recent species of the cribriomorph genus *Corbulipora*, *C. inopinata*, is described from several localities in the western part of the Great Australian Bight. All species of *Corbulipora*, both Recent and fossil, are known to occur in several phases. The form of the subcolonies, and the characters of the component zooids may be very different in each phase, and subcolonies are capable of separate existence. *C. inopinata* occurs in an encrusting phase, in a flustriform, ovicellate phase, and a bilaminar rooted phase. All zooids have some form of cribriomorph frontal shield, unlike some of those of the closely related *C. tubulifera*. The shield has, however, different characters in each phase.

A NEW SPECIES OF MULTIPHASED *CORBULIPORA* MACGILLIVRAY, 1895 (BRYOZOA: CRIBRIOMORPHA) FROM SOUTHWESTERN AUSTRALIA.

P. E. BOCK & P. L. COOK

BOCK, P. E. & COOK, P. L. 1998. A new species of multiphased *Corbulipora* MacGillivray, 1895 (Bryozoa: Cribriomorpha) from southwestern Australia. *Records of the South Australian Museum* **30**(2): 63–68.

A new Recent species of the cribriomorph genus *Corbulipora*, *C. inopinata*, is described from several localities in the western part of the Great Australian Bight. All species of *Corbulipora*, both Recent and fossil, are known to occur in several phases. The form of the subcolonies, and the characters of the component zooids may be very different in each phase, and subcolonies are capable of separate existence. *C. inopinata* occurs in an encrusting phase, in a flustriform, ovicellate phase, and a bilaminar rooted phase. All zooids have some form of cribriomorph frontal shield, unlike some of those of the closely related *C. tubulifera*. The shield has, however, different characters in each phase.

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The occurrence of distinct phases of correlated colony growth form and zooid morphology in species of *Corbulipora* has been described in some detail by Bock and Cook (1994; in press). Essentially, the function of the phases appears to be the same in all species. The first, ancestrulate phase is minute, encrusts shells and shell fragments, and may even have an interstitial existence. It establishes the colony and results from the settlement and metamorphosis of a motile larva. The second, erect phase is cellularine or flustrine, and arises from stalk-like kenozooids and autozooids growing from the peripheral pore-chambers of the zooids of the primary phase. This phase develops ovicells and large interzooidal avicularia. The second phase gives rise in various ways to a small, bilaminar or frontally budded third phase, which is known, in Recent species, to be anchored by numerous rhizoids. As the ovicelled second phase tends to be thinly calcified, the delicate subcolonies may easily be destroyed, or at least detached from their origins. The bilaminar phase maintains the position of the colony and develops further ovicellate subcolonies, which may be able to alternate with it more than once (Bock & Cook in press).

Collections of bryozoans, made by the R.V. Franklin, using an epibenthic sled, from localities in the western Great Australian Bight in July 1995, have produced a wealth of specimens and

species. These include subcolonies of *C. tubulifera* and of an undescribed species of *Corbulipora*, which has several distinctive features.

MATERIALS AND METHODS

Specimens are stored in the Collections of the Museum of Victoria (MOV) and South Australian Museum (SAM). Specimens for scanning electron microscopy were coated with gold.

The Stations from which specimens of *Corbulipora* were obtained were as follows:

C. inopinata sp. nov.

GAB 118 34°59'S, 119°00'E, 85m. Young non-ancestrulate colonies encrusting worn adeonid and lunulite colonies of bryozoans.

GAB 098 34°39'S, 122°26'E, 156m. 1 phase-2 subcolony with numerous avicularia.

GAB 093 34°32'S, 122°58'E, 95m. 1 phase-1 subcolony and 1 phase-2 subcolony with ovicells.

GAB 083 34°21'S, 124°08'E, 180m. 2 phase-1 subcolonies encrusting *Turritella* shells.

GAB 049 33°53'S, 125°22'E, 156m. 4 phase-2 subcolonies, developing into phase-3 at tips, one repeating phase-2.

GAB 056 33°19'S, 125°43'E, 73m. 2 large phase-

2 subcolonies, one with ovicells, developing from phase-3 subcolonies.

GAB 045 33°25'S, 125°58'E, 143.5m. 3 small phase-3 subcolonies with stalks.

GAB 020 33°20'S, 129°18'E, 157m. 9 small phase-2 subcolonies, 2 developing from phase-3 subcolonies.

GAB 013 33°06'S, 130°00'E, 101m. 2 phase-2 subcolonies, one with ovicells, and one phase-3 with numerous rhizoids and one phase-2 subcolony.

GAB 014 33°16'S, 130°00'E, 155m. 2 phase-3 subcolonies developing into phase-2 subcolonies, plus 5 isolated stalks.

C. tubulifera (Hincks)

GAB 019 33°22'S, 129°19'E, 301m. 7 phase-2 subcolonies, and 2 phase-3 subcolonies.

SYSTEMATICS

Order Cheilostomatida Busk, 1852

Superfamily Cribrilinoidea Hincks, 1879

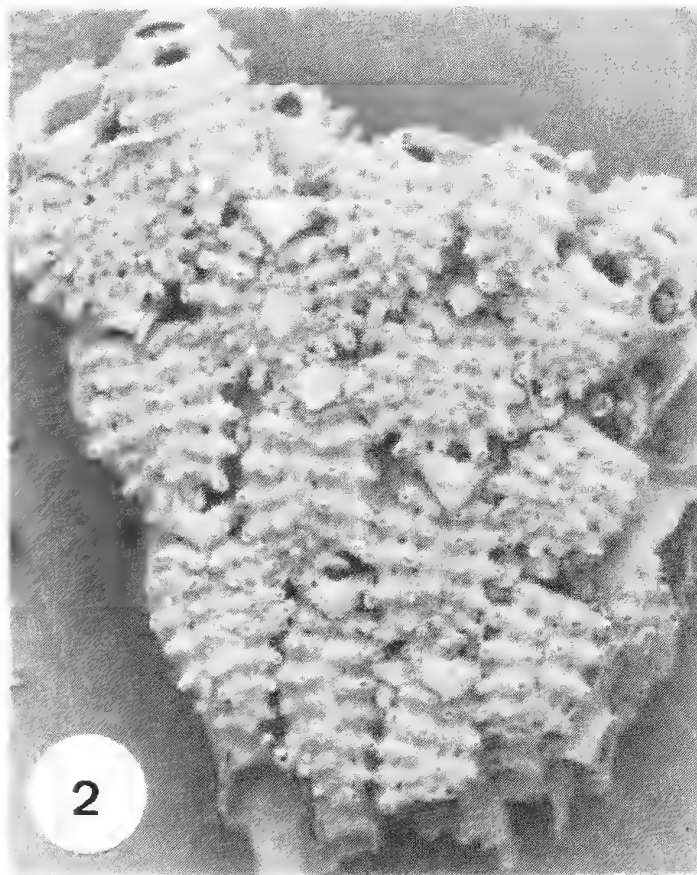
Family Cribrilinidae Hincks, 1879

Genus *Corbulipora* MacGillivray, 1895

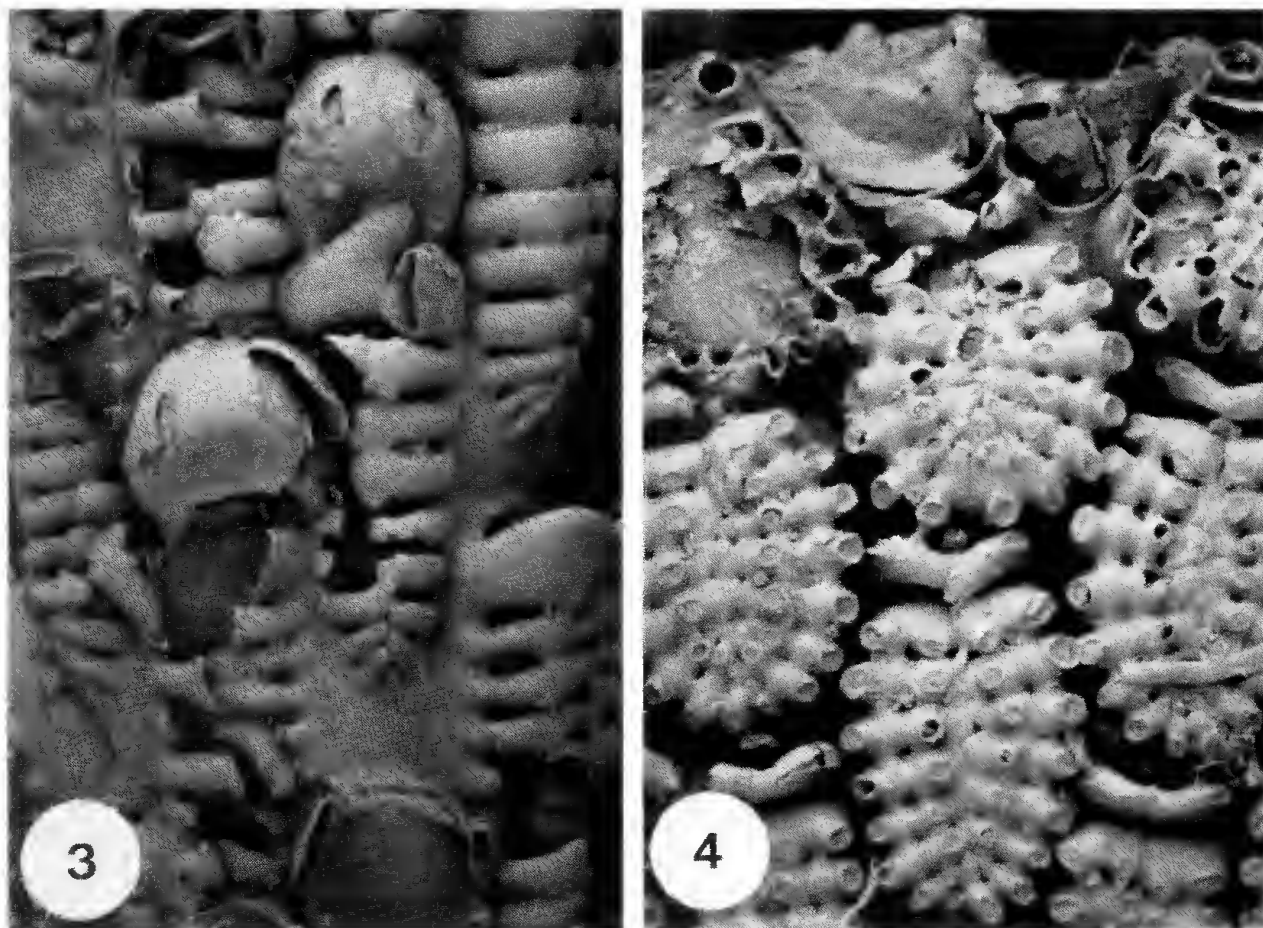
Corbulipora MacGillivray, 1895:60; Wass 1975:168; Bock & Cook, 1994:33; in press.

Corbulipora inopinata sp.nov.
(Figs 1–6)

Material Examined: HOLOTYPE MOV, F80665, GAB Stn 049, subcolony including phase-2 developing into phase-3 and then repeating phase-2.



FIGURES 1–2. *Corbulipora inopinata* sp.nov. 1, subcolony showing phase-2 autozooids and two ovicelled zooids at the proximal end (arrowed). Intermediate zooids leading to two astogenetic generations of phase-3 zooids at the growing tip (GAB Stn 049) X22; 2, phase-3 subcolony with marginal pore chambers and autozooids with occluded orifices (GAB Stn 020) X40.



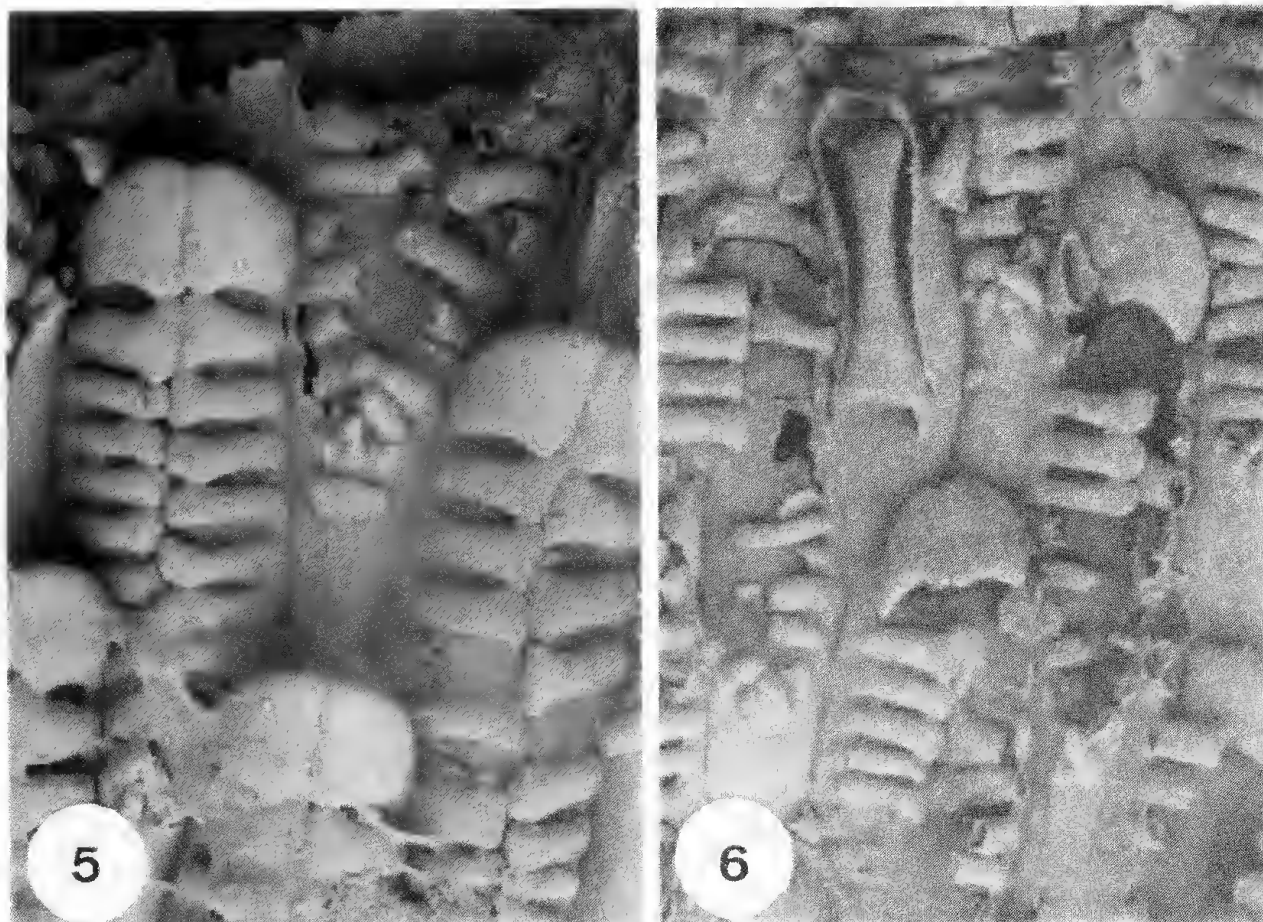
FIGURES 3–4. *Corbulipora inopinata* sp. nov. 3, phase-2 zooids with ovicells and simple frontal spines (GAB Stn 049, see also Fig. 1). X80; 4, phase-3 zooids with complex frontal shields (GAB Stn 049, see also Fig. 1) X70.

Paratypes: Rest of material, including SAM L755, GAB Stn 049 part.

Description

Corbulipora with colony including three subcolony phases. Primary phase encrusting, ancestrula not seen; primary triad zooids with frontal shield of 16 simple spines. All zooids with a distinct, smooth gymnocyst, and communicating through small pore-chambers. Remaining primary-phase zooids with frontal shields with 16–18 spines, separated by 3–4 series of small lacunae and with two concentric series of raised pelmatidia. Calcified orifice with 3 spines, lateral pair often bifid. Second, flustrine phase inferred to arise from primary phase. Fronds developing from stalk kenozooids and elongated autozooids, often in quadriserial groups; series bifurcating to form fronds 10–12 zooids wide and 150 astogenetic generations long, bifurcating up to 4 times. Autozooids with distinct gymnocyst and 14–16 flattened spines

overarching the frontal membrane. Brooding zooids with enlarged, curved, sometimes medially fused oral spines and large hyperstomial ovicell. Ovicell frontal with median suture and paired entoecial areas. Avicularia scattered, rare in presence of ovicells. Rostrum elongated, narrow, not raised distally; slightly expanded and rounded terminally, mandible hinged on a delicate bar, orientated distally. Tips of fronds with 3–4 astogenetic generations of zooids with intermediate morphologies leading to the third, bilaminar phase subcolonies. These form small, expanded groups of zooids with shields similar to phase-1 subcolonies, with two concentric series of raised pelmatidia. Zooids have a small orifice, sometimes partially occluded by the fusion of enlarged oral spines. Numerous rhizoids develop from marginal pore-chambers, together with stalk kenozooids and elongated stalk autozooids with a small opesia and marginal spines, which are the origin of repeated subcolonies of phase-2.



FIGURES 5–6. *Corbulipora inopinata* sp. nov. 5, phase-2 autozooids, note enlarged pair of distal spines (GAB Stn 098) X100; 6, phase-2 autozooids and avicularium (GAB Stn 098) X80.

Etymology

Inopinus L. — unexpected: referring to the occurrence of a second Recent species of *Corbulipora* with multiphase growth.

Remarks

The three phases of *C. inopinata* resemble those of *C. tubulifera* closely, but differ in several respects. The most noticeable difference is in the occurrence of a spinous shield in the autozooids of the second, flustrine phase. The spines are flattened and generally do not fuse centrally, although the enlarged suboral spines of marginal zooids may be fused. In addition, the avicularia of *C. inopinata* are much narrower, and are not raised distally, as are those in *C. tubulifera*, and the mandibles are hinged on a delicate, but complete bar. The palate is much longer in proportion to the proximal gymnocyst than in *C. tubulifera*. Other differences are small, but distinct and consistent. Although no ancestrula has been preserved, one of the small, phase-1 colonies encrusting *Turritella* from Stn GAB 083

possesses a post-ancestrular triad of very small zooids. These all have a shield of simple spines, very similar to the one post-ancestrular zooid of the triad in *C. ornata* (Bock & Cook, in press, fig. 1). Subsequent zooids have two series of pematidia, which do not develop until later in astogeny in *C. tubulifera*. The orifices of this stage are also wider than those of *C. tubulifera*. No stalk zooids have been preserved arising from the encrusting phase in *C. inopinata*, but by analogy with *C. tubulifera*, these are presumed to be identical with those which arise from phase-3 bilaminar subcolonies. These consist of one or two pairs of kenozooids 2.5mm long, often accompanied or succeeded by one or more pairs of elongated zooids 2mm long, each with a small opesia surrounded by 8–12 short, simple spines. Thus the stalks differ from those of *C. tubulifera* in being more robust, with more zooidal elements, and in the occurrence of autozooids with an opesia, rather than kenozooids, early in astogeny. The zooids of intermediate morphology at the tips of the flustrine phase-2 fronds attain a complete

shield of phase-3 autozooids within 4 astogenetic generations. First, the flattened spines fuse medially, leaving a row of small lacunae. A single series of pematidia develops on the spines of the next generation of zooids, and a paired series, with 3–4 lacunae, develops on the shields of subsequent generations. The small calcified orifice is complete within the next generation or two. Although the general appearance of the autozooids of the bilaminar phase is very like those of *C. tubulifera*, they have a smaller orifice. Although these are often partially occluded by the oral spines, they do not usually exhibit the series of changes resulting in complete closure of the orifice which occurs in *C. tubulifera* (Wass 1975). In one specimen from GAB Stn 020, the spines are enlarged and nearly occlude the orifice (Fig. 2).

One of the specimens from GAB Stn 013 illustrates the relationship and probable functions of phase-2 and phase-3 subcolonies particularly well. It consists of a small bilaminar phase-3 subcolony comprising approximately 60 autozooids. More than 50 rhizoids arise from the marginal pore-chambers, and on one face of the subcolony these are involved with and adhere to minute shell and bryozoan fragments. On the edge of the other face, one quadriserial stalk, 15mm

long, consisting of two generations of quadriserial kenozooids and 10–12 generations of elongated autozooids, gives rise to a phase-2 flustring subcolony about 30mm long, with more than 40 astogenetic generations. It seems almost certain that the one face of the bilaminar phase was buried in the surface sediments, whereas the flustring frond extended above the surface. This subcolony is quite small; two flustring subcolonies from Stn 056 extend up to 70mm and include 10,000 to 12,000 zooids, many of which are ovicelled. These would protrude well above the surface of the bottom sediment, allowing the larvae to be released easily.

The similarities in phase structure found in *C. inopinata* and *C. tubulifera* reinforce the inferences previously made by Bock and Cook (1994; in press) as to the nature and relationships of the known phases in *C. ornata* and *C. suggerens*, from the Victorian Tertiary. They also strongly suggest that the ovicellate phase of *C. suggerens* was a thinly calcified cellularine subcolony type, which has not been preserved as a fossil.

C. inopinata occurs in the western Bight together with *C. tubulifera*, but from shallower waters. In Bass Strait, and from Tasmania, *C. tubulifera* is known from a wide range in depth from 40m to 800m. It appears to be at the limits of its range south east of Eucla, in deep water. Wass (1975) first described *Corbulipora oriparma*, which is the bilaminar phase of *C. tubulifera*, from three localities. The holotype was from northeast Tasmania, the other specimens were from the eastern part of the South Australian coast. Subsequently, Wass and Yoo (1983) recorded *C. oriparma* from 12 localities, extending from near Perth to southwest of Eucla. These are similar to many of the localities from which specimens have been recently examined, and which have produced *C. inopinata*. None of Wass and Yoo's (1983) localities was from a greater depth than 158 m, far shallower than the most westerly known locality for *C. tubulifera*. Only examination of the specimens recorded by Wass and Yoo (1983) can decide their identity.

ACKNOWLEDGMENTS

We should like to thank Dr Yvonne Bone (University of Adelaide) and the Master and crew of CSIRO R.V. 'Franklin' for the opportunity for one of us (P.E.B.) to take part in the sampling programme in July 1995, which led to the discovery of the species described here. We are also grateful to Mr D. McDonald for his help in preparation of this paper.

TABLE 1. Comparative measurements in mm of *Corbulipora inopinata* sp.nov. and *C. tubulifera* (Hincks). Lz, lz length and width of autozooid; lo, width of orifice; Lov, lov, length and width of ovicell; Lav, lav, length and width of avicularium; Lp, length of avicularian palate.

Character	<i>C. inopinata</i>	<i>C. tubulifera</i>
Phase 1 (including primary zooids in mms)		
Lz	0.41 – 0.70	0.45 – 0.74
lz	0.35 – 0.50	0.38 – 0.50
lo	0.12 – 0.17	0.10 – 0.13
Phase 2		
Lz	0.98 – 1.30	0.78 – 1.32
lz	0.26 – 0.29	0.25 – 0.33
Lov	0.21 – 0.23	0.23 – 0.27
lov	0.24 – 0.26	0.28 – 0.33
Lav	0.60 – 0.75	0.65 – 0.96
lav	0.15 – 0.17	0.22 – 0.26
Lp	0.43 – 0.51	0.31 – 0.35
Phase 3		
Lz	0.50 – 0.75	0.54 – 0.87
lz	0.37 – 0.50	0.32 – 0.54
lo	0.09 – 0.10	0.10 – 0.14

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THE ARCHAEOLOGY OF LAKE SYSTEMS IN THE MIDDLE COOPER BASIN, NORTH-EASTERN SOUTH AUSTRALIA.

ELIZABETH WILLIAMS

Summary

This paper presents the final report of a study of the archaeology of a number of lake systems located in the middle section of the Cooper Basin and neighbouring areas near Innamincka, South Australia. The paper outlines the results of archaeological fieldwork carried out during 1987 in one area within the region and relates this to other research undertaken in 1986 and 1989 in other parts of the middle of the Basin.

THE ARCHAEOLOGY OF LAKE SYSTEMS IN THE MIDDLE COOPER BASIN, NORTH-EASTERN SOUTH AUSTRALIA.

ELIZABETH WILLIAMS

WILLIAMS, E. 1998. The archaeology of lake systems in the middle Cooper Basin, north-eastern South Australia. *Records of the South Australian Museum* 30(2): 69–91.

This paper presents the final report of a study of the archaeology of a number of lake systems located in the middle section of the Cooper Basin and neighbouring areas near Innamincka, South Australia. The paper outlines the results of archaeological fieldwork carried out during 1987 in one area within the region and relates this to other research undertaken in 1986 and 1989 in other parts of the middle of the Basin.

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The lakes forming the main focus of this study are located within an extensive linear dunefield, the Strzelecki desert, which forms part of Australia's continental dunefield. Although archaeological research has been undertaken along the main channel of the Cooper in the middle Cooper basin, particularly the Innamincka area (Hughes & Lampert 1980, McBryde 1987), the archaeology of the region's series of lake systems had not been studied until this research programme. Given that at least a number of the lakes hold fresh water for some considerable time, and that this is a strikingly unusual feature of arid areas generally, it is very likely that the lakes would have been the major focus of occupation for at least the recent period and possibly for extended periods in the past. As well, it is possible that landforms associated with the lakes such as source-bordering dunes preserve information about Pleistocene climates and changing environmental conditions, and possibly also about Pleistocene human occupation. A study of the lakes therefore had the potential to contribute to our knowledge of not only the recent occupation of the region but also that of past settlement, and possibly, the wider question of how Australia's arid zone itself was occupied.

In structuring the project, a preliminary analysis of the region revealed considerable variation of the nature and types of lakes. The study was designed to examine this variability in relation to human settlement. The study was designed as follows. I examined the archaeology of examples of the three major types of lake systems in the region. These are the semi-permanent lakes of the Coongie system, fed by the Cooper's North-West

Branch; small isolated salt lakes marking the edge of the Cooper Basin, and a series of ephemeral lakes to the north of the Basin fed by local drainage and precipitation. The results of this work are presented below. In the latter sections of my discussion I compare this information with that obtained from sites located in a relatively waterless core of the dunefield located in the southern part of the Strzelecki desert. The concluding part of the paper outlines a number of speculative hypotheses about the occupation of the region and of Australia's arid zone in general.

Work carried out in the Coongie lake system has previously been reported on in Williams (1988) and that undertaken in the Strzelecki dunefield summarised in Smith, Williams and Wasson (1991). The current study draws this research together to present a comprehensive view of the region's archaeology.

GENERAL ENVIRONMENTAL FEATURES OF THE REGION, INCLUDING THOSE IMPORTANT FOR HUMAN OCCUPATION

The study area lies in one of the most arid parts of Australia. The region is covered by an extensive linear dunefield and receives the lowest rainfall reading of any area of the continent (125 mm per annum). Despite the aridity there are reliable water sources here in the form of the Cooper Creek channel, its overflow system – the North-West Branch, and associated lakes fed by the channel systems. The amount of water in this drainage complex does not reflect local rainfall patterns and predominantly derives from received precipitation falling many hundreds of kilometres

to the north-east during the wet season in the upper parts of the Cooper catchment in north-west Queensland.

Given the arid setting of the region, water was a valuable resource and one of the most important features for human occupation. This is confirmed by the distribution of archaeological material within the Coongie lake system – site size and stone artefact density increases in relation to the location of permanent and semi-permanent water sources (Williams 1988: 59).

Another important feature for occupation was the availability of good quality stone suitable for artefact manufacture. Stone sources are extremely localised here and are either scarce or entirely absent within most of the linear dunefield itself. Some stone is available in the form of pebbles carpeting the surface of the gibber plains or 'stony deserts' located on the edges of the study area but this source only exists in the form of small nodules, not necessarily suitable for all types of artefact manufacture. The most extensive areas of stone are found in outcropping areas of hard rock within areas of dissected tablelands located on the margins of the study area.

Although the availability of resources such as water and stone were crucial, the two resources do not always coincide geographically. In the area immediately surrounding Innamincka where are found the extensive deep waterholes of the main Cooper channel and the abundant good quality stone resources of the locality's mesas and dissected tablelands, the two resources are abundant and lie close together. In the Coongie lakes system located within the stone-free linear dunefield, although water resources are extensive, good quality stone lies at least 60 km away. Therefore one of the major features of the archaeology of the region relates to how people balanced their need for stone with that for water and how this varied from one area to another. Because this feature is responsible for much of the patterning of the archaeology of the Basin and neighbouring areas, it is the major focus for this study.

A second and related focus concerns the antiquity of human occupation of the region. This topic is reported on in detail in Smith, Williams and Wasson (1991) and is also discussed here.

The structure of the paper is as follows. Given that the environment places such strong constraints on human occupation in the region, a general overview of climatic and geographic data is presented first, including material on environmental chronologies. This is followed by a

brief summary of historical accounts of how Aboriginal people were observed to be using the area at the time of European contact, in order to present a picture of the occupation of the area at least for the recent past. The paper then reports on archaeological sites investigated, including an analysis of stone artefacts from a selected sample of sites. I conclude with a brief discussion of some of the theoretical implications of my work.

THE CONTEMPORARY ENVIRONMENTAL SETTING

A number of the environmental parameters for the region have already been presented in Williams (1988). This section does not repeat this material and instead provides more detailed information on localities previously discussed and new data on areas not referred to in other publications.

The main focus of the study area is a series of lake systems within the Strzelecki desert. On the east and west the Strzelecki is bounded by stony country, comprising gibber plains and areas of dissected tablelands. The latter consists of the low, but locally steep escarpments and small mesas of the geological features known as the Innamincka and Cordillo domes.

The aridity of the area has been noted above. Precipitation in the region is unpredictable and erratic, with no systematic seasonal patterning. Evaporation is extremely high, at least one order of magnitude greater than precipitation (Reid and Gillen 1988: 16).

Three of the lake systems which form part of the study area are discussed in some detail here. They are the freshwater lakes of the Coongie system, a ring of salt lakes which mark the boundary of the Cooper drainage system, and another chain of lakes which lie to the north of the system and to the west of Cordillo Downs station. For convenience I refer to this latter group of lakes as the 'Cordillo lakes'.

The Coongie system

The Coongie system comprises a series of large, shallow, irregularly-shaped lakes lying within the linear dunefield. The lakes are fed by a tributary of the Cooper, the North-West Branch. The system has a complex hydrology and is described here in its constituent sections from south to north. Closest to the North-West Branch feeder channel are three lakes: Coongie, Marroocoolcannie and Marroocutchanie, which are fed directly from the North-West Branch. Two lakes lying further

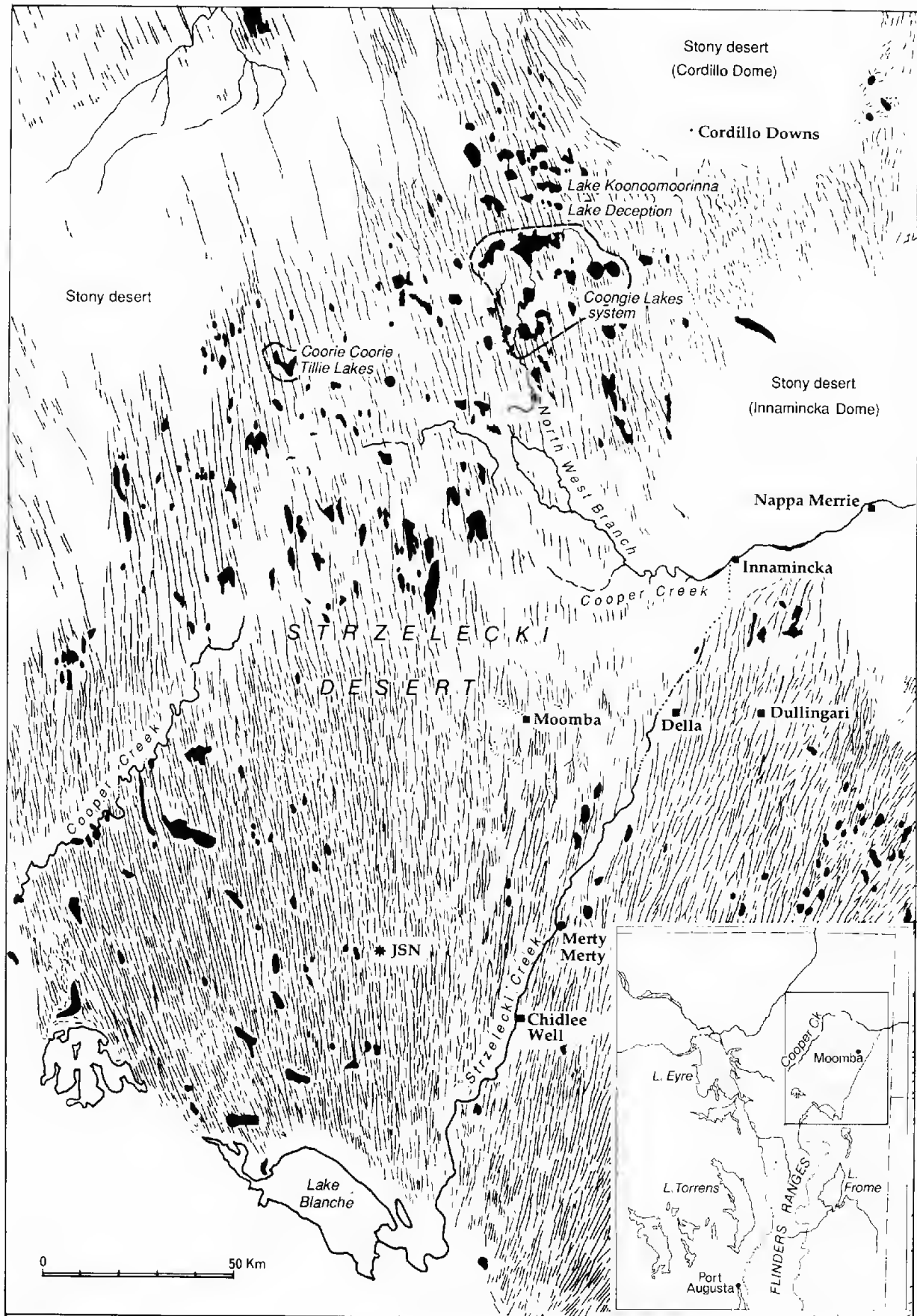


FIGURE 1. Regional map of north-east South Australia showing the sites mentioned in the text.



FIGURE 2. Map of the Coongie and Cordillo lake systems.

north, Toontoowaranie and Goyder, are fed by interconnecting creeks from overflow from the first three lakes. To the north again are a further three lakes: Marradibbadibba, Lady Blanche and Sir Richard, which fill from overflow from Lake Goyder. In this paper I refer to all of the lakes collectively as the 'Coongie system'.

A further series of lake and channel systems also have some connection either to the Coongie system or the North-West Branch channel. It is noted that although they do hold water at certain times (as observed by the explorer, John McKinlay in 1862), the Coongie system, at least in the recent past, held the most extensive and most reliable sources of water. Little is currently known about their hydrology and for this reason the lakes do not form part of this study.

The North-West Branch which joins the Cooper west of Innamincka diverts most of the flow of the main Cooper channel northwards. For the area west of Innamincka relatively little water thus flows down the main Cooper channel on to Lake Eyre (Mike Steele, Innamincka store, pers. comm.). The Coongie system therefore catches most of the water coming down the Cooper channel. Flow down the Cooper derives from two sources: local precipitation and received rainfall which falls as far as 500 km upstream in the channel country of western Queensland. This latter precipitation falls mostly during the summer monsoon and contributes the major portion of the Cooper's flow. In contrast to local rainfall its timing is relatively predictable. Water from the summer monsoon rains takes about three months to come down the channel, first reaching the Coongie about late autumn (Barry Saunders, Innamincka region, pers. comm.).

Despite this level of predictability, the amount of water which actually comes down the channel and the exact time of year when it arrives markedly fluctuates in relation to variability in the timing and effectiveness of rainfall in the upper Cooper catchment. Nonetheless, there are predictable water sources in the form of deep, permanent waterholes which are often a couple of kilometres in length, located along the channels of the main drainage systems such as the Cooper and the North-West Branch.

With the possible exception of Coongie, the lakes do not hold water on a permanent basis. Oral tradition amongst current residents of the Innamincka region suggests that Coongie Lake itself holds water for most of the year, although the nature and amount of water it holds is difficult to quantify because of a lack of historical records.

The other lakes in the system hold water for months at a time but the extent and duration is highly variable and depends on a number of factors. These include the amount of water coming down the Cooper from rainfall in the northern catchment, local precipitation, the position of the lake relative to the North-West Branch and the season of the year (evaporation is highest during summer).

Despite variability in the amount of water held in the Coongie system, the presence of often extensive supplies of fresh water in an otherwise extremely arid environment is extremely rare within Australia. The region consequently supports a very productive and diverse ecology, but one which varies in relation to water levels in the lakes and channels. The variability does not decrease overall productivity, and in fact is responsible for the high biodiversity of the region. The chain of lakes, with its complex sequence of rising and falling water levels is biologically highly productive. The lakes provide a diverse range of constantly changing habitats and have the potential to support the largest number and widest range of resources in the region. The major resources found here are: birds, especially waterbirds; fish, crayfish and mussels; dry-land and aquatic plants, and some mammal species.

Biological studies of the system reveal this very high productivity (Reid and Gillen 1988, Reid and Puckeridge 1990). Reid and Gillen for example recorded 161 separate bird species in the Coongie system and estimated that during the year under study (1986 – a wet year when all lakes in the system held water for much of the time) 20 000 waterbirds permanently occupied the lake chain. (1988: 184, 198).

Because of the interconnectedness of the system, rising and falling levels in one lake affect other lakes in the chain. Given that most of the plant and animal species in the region are oriented to specific environmental niches, variation in water levels consequently provides a much wider range of habitats than would otherwise be available along a permanent waterhole where water levels remain relatively constant. For example, although water levels in one lake may begin to fall with evaporation, certain species of waterbirds whose habitat is that of more shallow water will migrate in to the lake while those whose habitat is that of deeper water will move to another lake where water levels are rising. The differential fluctuation of water levels means that the lakes have the potential to carry the largest biomass of plants and animals in the region

because they are providing a wide range of ecological zones. The permanent waterholes on channels and rivers carry a relatively lower biomass because their environments are much less variable. Water levels fluctuate significantly less in these deep waterholes, supporting a smaller, but more predictable range of resources.

Salt lakes or 'salinas'

These irregular-shaped lakes lie in a ring along the northern and western boundary of the Cooper drainage basin and mark the boundaries of that system. They are located in the midst of the linear dunefield and are deflation hollows cut to groundwater level. This type of feature has been termed a 'salina' (Macumber 1980). Their salinity derives from the fact that in the region the groundwater is saline. Although no hydrological studies of the salinas in this area have been undertaken, it appears that for the recent past at least, they are permanently saline. In contrast to the Coongie system they therefore support relatively few plant and animal resources.

The Cordillo lakes

To the north of the Coongie system, beyond the salt lakes, lie another series of irregularly-shaped lakes. As with the salinas, no formal studies of these have been undertaken and there are no records of how often they fill.

Cartographic and field observations of the locality suggest that there are at least ten lakes in the system, connected by a series of channels. It appears that they fill from local run-off from the stony country of the Cordillo dome to the east. Their hydrology, unlike the Coongie system, therefore reflects local precipitation. The lakes were dry when fieldwork in the area was undertaken (1987), despite the years 1986 – 1987 having been much wetter than average in terms of local rainfall. This suggests that considerable local precipitation is required to fill them and they thus remain dry for very long periods of time. They are not salinas though, and small pools of fresh water were present in 1987 in a few places along the channels linking the lakes. The predominantly dry character of the lake system suggests that it supports relatively few plant and animal resources in comparison to the Coongie, but the presence of some areas of freshwater indicates that more resources are supported than the saline lakes.

The region's current environment is not necessarily the same as today as in the past. Over time there have been significant changes in climate, hydrology and landforms, with

consequent effect on the human occupation of the region.

PAST ENVIRONMENTS – DUNEFIELD AND FLOODPLAIN RESEARCH

Much of the information on past regional climates has been summarised and presented elsewhere (Williams 1988) and so here I briefly refer to this work and also discuss new data which has arisen as a result of the study. R. Wasson has developed an environmental chronology for the region, based on stratigraphic sequences derived from longitudinal dunes and floodplain sediments (for references see Williams 1988). A summary of his findings and a discussion of their implications for the hydrology of the lakes follows.

Wasson's work indicates that before 22 000 years ago the Cooper had a higher velocity than today and was flooding out to a much greater extent. Although geomorphological studies of the Coongie lakes themselves have not been undertaken, Wasson's data suggest that if the Coongie system was in operation during this period it would have held considerably more water than today. As well, groundwater levels for the region as a whole would have been higher, indicating that the lake depressions which are now salinas may have held fresh water. Current work does not indicate whether local precipitation was also high at this time, so that it is not possible to model processes which may have been occurring in the Cordillo lakes.

Around 22 000 years ago, the Cooper's velocity decreased, flooding of the outer floodplain decreased and it is likely that the water table lowered as well. Consequently it is likely that what are now salinas would have changed from fresh water at this time. Lake levels in the Coongie system may have become lower. About 20 000 years ago conditions were windier and more arid, activating a period of dune building throughout the linear dunefield. The dune sediment was drawn from the deposits formed from the continuing, reduced flooding of the outer floodplain. These climatic conditions and the consequent dune building persisted until around 16 000 years ago. At about 12 500 years ago the flooding-out of the outer floodplain ceased, removing the sediment available for dune building.

Dune building began again in the later Holocene, although on a smaller scale than in the late Pleistocene. Wasson (1986: 79) notes that this event is enigmatic, since in contrast to the late

Pleistocene there seems to have been no climatic change occurring on a scale large enough to be able to mobilise sediments. He has speculated that it is possible, although not yet conclusively demonstrated, that the phenomenon could be related to more intensive human occupation of the region. If such intensive occupation took place, the erosion resulting from Aboriginal firing of vegetation to aid the procurement of food resources, together with clearing of trees and other vegetation to provide fuel for campfires and earth ovens, may have caused greater mobility in sediments.

PAST ENVIRONMENTS - STUDIES OF LAKESHORE FEATURES

The environmental data presented above is derived from a study of dunefield and floodplain sediments and presents a broad regional chronology. Is it possible to develop a chronology for the lake systems themselves?

A formal study of the geomorphology of the lake systems was beyond the scope of this study so I developed a smaller project, more complementary to the archaeological work. This involved an examination of whether landform features such as source-bordering dunes, which have the potential to contain information on lake chronology, had developed on lakeshore margins. These transverse dunes, Twidale's 'leeside mounds' (1972: 85-86), are similar to the lunettes of semi-arid regions. They are formed when longshore drift transports debris to beaches or lee shores of lakes. This sediment is then locally redistributed by the wind before being trapped by vegetation close to the lake margin.

The work was complementary to the archaeological survey in the sense that it was anticipated that source-bordering dunes were also likely to be a focus for human occupation. Systematic survey of these features would not only have the potential to reveal information about environmental features but also about human occupation, and the chronology of such occupation.

The project comprised an examination of examples of source-bordering dune features for each of the lake systems discussed earlier. Aerial photographs were used to identify the features and distinguish them from the linear dunes of the continental dunefield. The transverse dunes are paler in colour and generally trend east-west in contrast to the north-south longitudinal dunes.

Once they were identified on the aerial photographs I travelled to them on the ground and systematically surveyed all exposures for any archaeological material.

Access to the features by vehicle was often difficult and in a number of cases access was by helicopter. Regarding the dating of the dunes it is noted that at the time the work was undertaken only radiocarbon dating was available to the study. Thus if organic material suitable for such dating was not present in-situ the dunes were unable to be directly dated. The results of the work are presented below.

The Coongie system

Information on a number of the source-bordering dunes of the Coongie system is outlined in detail in Williams (1988: 58-60). A summary of the work is presented here along with new data on other parts of the system.

The analysis of aerial photographs, maps and the survey work itself revealed that while some features such as colour of the source-bordering dunes are similar across the system there is major variability in the number, size and location of the features. A common feature is that all dunes are pale in colour and have little or no carbonate formation within their profiles, and they contain intermittent scatters of artefacts on their surface - typologically the artefacts appear to be late Holocene in age. All of these factors suggest the dunes are recent features. When cores of the dunes were exposed by erosion and these sections were examined, no organic or archaeological material was found in-situ, with the exception of one site at Lake Marradibbadibba - Lake Goyder 1. Details of this site are presented in Williams (1988: 60) where it is noted that it dates to the relatively recent past - 810-130 BP (ANU 5424) thus confirming the recent age of the transverse features.

There is considerable variation in dune shape and alignment across the system. Some lakes had a low and amorphous single transverse dune (such as Toontoowaranie); others had a higher and more distinct single dune (Coongie, Marroocoolcannie). Still others had multiple transverse dunes, one behind the other (five in the case of Lake Lady Blanche, yet none on the neighbouring Lake Sir Richard, and five or more in the floodplain between Coongie and Toontoowaranie). Location of dunes relative to lakes ranged from north, to north-east and east.

Given that the study of the dunes was only a preliminary one, it has not been possible to

determine what factors are responsible for the variation in dune features. It is likely that since there is major variation in the shape and size of the lakes themselves and how they fill relative to channel features and other lakes, and marked fluctuations in the amount of water coming into the system and the timing of when these events occur, it is probable that these factors are responsible for much of the variation.

The morphology and colour of the dunes indicates that they are of late Holocene rather than Pleistocene age. Two hypotheses could explain their recent age. The first proposes that the lake system was active in the Pleistocene, but since it is still in operation today, receiving what can be major flows of water and often flooding out extensively, any Pleistocene shore features have either been swept away by previous high-water events or are well buried below flood deposits. In 1974 for example, the entire system flooded out – aerial and satellite photography reveals water extending for hundreds of square kilometres with only the tops of linear and transverse dunes visible. Krieg and Callen note that the Coongie system is one of net sediment accumulation (1990: 60) and it is thus possible that many older lake-shore features have been disturbed or buried by sedimentation.

The second hypothesis proposes that the lake system may not have been in operation in the Pleistocene. Recent work by Callen and Bradford (1992) presents data showing that the current situation, in which most of the flow down the Cooper channel west of Innamincka is diverted north up the North-West Branch, may be very sensitive to minor changes in topology resulting from such factors as tectonic activity or shifts in sedimentation or the location of dune features (transverse and longitudinal). Slight movements on faults or in sedimentary features of only 1–2 metres within a large, low angle fan formed by the Cooper immediately west of Innamincka may be sufficient to create major changes in channel direction, and thus whether the Cooper flow is diverted either along the Branch, along another channel such as the main Cooper channel or even southwards down Strzelecki creek. Given this sensitivity to change it is possible that during the Pleistocene the North-West Branch may not have been carrying the main Cooper flow and the lakes may not have functioned as they do today.

Because a detailed study of the geomorphology of the Coongie system has not been undertaken it is not possible to resolve these competing hypotheses. It is nevertheless possible to conclude that whatever the reason, the lake-shore features

currently exposed within the area do not provide a window onto the Pleistocene.

The salt lakes

Two of the larger salinas in the region, Coorie Tillie and Lake Deception, were chosen for analysis. Although the lakes lie some 100 km from each other, the form of their transverse dunes is virtually identical, in direct contrast to the variability of the Coongie system. As well, the transverse dunes themselves are very different to those of the Coongie.

Each lake has a low, flat, pale-coloured transverse dune on its northern edge. These have been extensively gullied to expose older-looking sediments which are redder in colour and more compact, with a pronounced carbonate horizon. It is likely that further analysis would confirm that the sediments are of Pleistocene age.

A systematic survey of the length of each dune, including an examination of the many sections of dune core exposed by erosion, revealed that the small amount of archaeological material present all lay within recent sediments on the dune surface, rather than in the Pleistocene core.

In contrast to the Coongie, there are no large amounts of water coming into the system to modify or distort landform features. The salinas are groundwater features, and do not fill from any channels. The dunes' consistency in nature and form could result from similarity in formation and hydrology operating on the lakes. Unlike the Coongie, the transverse dunes appear to have the potential to preserve Pleistocene sediments but no stratified archaeological material is currently visible within their profiles.

The Cordillo lakes

This system has a set of source-bordering dunes different from both the Coongie system and the salinas. Like the salinas and unlike the Coongie system, there appeared to be a strong consistency in the number, form and structure of the features across the lake margins.

On the northern edge of the lakes is a sequence of three transverse dunes trending east-west, and located one behind the other. The dune closest to the lake edge is quite low, less than a metre in height and pale in colour. Behind this is another, slightly higher, pale-coloured dune which is beginning to blow out into small longitudinal dunes. Behind this again is another higher dune, distinctly orange in colour with a pronounced carbonate horizon, which has almost completely blown out into longitudinal dunes.

The outermost dune is heavily eroded and it is likely that it is Pleistocene in age. Samples of carbonate from within the profile of the dune from Lake Koonoomorinna were dated using radiocarbon techniques and returned the relatively recent dates of 3930–80 BP (ANU 6182) and 4560–80 BP (ANU 6182). John Head of ANU Radiocarbon Laboratory notes that the samples are not dating the formation of the dune itself, only the last major phase of mobilisation of carbonates within the dune. Such mobilisation would have taken place during the last period of stable high-water levels in the region and the samples are probably dating this event (pers. comm.).

A complete survey of all of the dunes from one lake, Koonoomorinna, revealed that stone artefacts are scattered across the surface of each dune, but that no artefacts or organic material were present in-situ within the cores of the features, including the Pleistocene dune. An analysis of a number of samples of the artefacts is presented later in the paper but it is noted here that those seen had features characteristic of artefacts dating to the mid-late Holocene.

It is suggested that the regularity in source-bordering dune spacing and form for the Cordillo lake system is, like the salinas, reflecting consistency in processes involved in formation and filling. The lakes fill from run-off within the local catchment, and in contrast to the Coongie system there is significantly more regularity in their hydrological processes and many fewer flood events to affect the morphology of lake-shore features. Like the salinas and in contrast to the Coongie system, the transverse dunes appear to have the potential to preserve Pleistocene sediments but, as with the salinas, no in-situ archaeological material is currently visible within their profiles.

It is not known at this stage why the lakes preserve a group of three transverse dunes. Each dune may reflect a period of relative stability in lake levels so that the position of the dunes, one behind the other, may indicate a shrinking lake basin since higher levels in the later Pleistocene. Alternatively, the position of the dunes may reflect the fact that all lakes in the region, including the Coongie system, are slowly migrating southwards over time (Bob Wasson pers. comm.). The presence of the dunes may reflect both factors.

Following this presentation of climatic and environmental information, the next section places the region in a more recent context by summarising historical accounts of how

Aboriginal people occupied the area at the time of contact with European people. The section draws on information presented in Williams (1988) and Layton, Folcy and Williams (1991: 258–259) and also presents new material.

HISTORICAL ACCOUNTS OF SUBSISTENCE AND SETTLEMENT

Citing McKinlay (1862), who was the first European to travel through the entire middle Cooper lake system, the region was densely populated at the time of contact. McKinlay's expedition, which was one of those initiated to search for Burke and Wills, involved the party spending several months in the lake system in 1861–1862. During this time they were systematically examining each of the lakes and channel systems of the North-West Branch in their search for the missing explorers.

McKinlay saw more than 700 people in the region during his travels, including more than 300 people camped along Hamilton Creek, immediately west of Lake Toontoowaranic in the Coongie system, 200–300 people along the North-West Branch just south of Coongie Lake itself, and at least 150 people around Lake Lady Blanche (1862: 37, 38, 46). Because of the length of time he spent in the region he was also able to observe how people utilised fluctuations in water levels across the lakes.

McKinlay's information shows that population densities were highest around the large, permanent waterholes on the channels of the North-West Branch and the Cooper itself, and those lakes within the North-West Branch system which were currently holding water. Group composition appears to have been relatively fluid. Large aggregations of 150 or more were formed to take advantage of the flush of food resources which appeared as lakes began to fill. As they dried out again, people moved to other lakes, following the water, or split into small groups to harvest other resources or move on to other areas. Permanent or semi-permanent camps of between twenty and forty people were found along the permanent waterholes of the channel systems and this observation is also consistent with that of King, the surviving member of the Burke and Wills party who was cared for by Aboriginal people in the Innamincka region (Burke and Wills 1861). At these more settled camps habitations comprised substantial huts.

Important food resources were fish, crayfish

and mussels; waterbirds, and the variety of plant foods which germinated after flooding or local rain, especially nardoo. People favoured the lakes and rivers but after rain in the local catchment dispersed into small groups and travelled out into the drier dune country (McKinlay 1862: 49; Jones 1979). In these latter areas a flush of resources including small mammals, reptiles and certain types of plant foods, especially seed plants, appeared after the rain.

Although there are no ethnographic observations of how the Cordillo system was used, it can be hypothesised that after local rain areas such as this became a focus for occupation, the water sources it now held resulting in a relative abundance of food. It is also possible that if semi-permanent pools of water remained for a considerable time throughout the year in the shallow channels between the lakes, some small groups of people might have occupied the region on a more permanent basis.

While historical accounts mention the existence of the salt lakes there are no direct ethnographic observations of people using these areas. This implies that they were not favoured areas for occupation on a day-to-day basis.

Dealing with periods of resource stress

Although the Cooper lakes and channel systems contain a large range of food resources for much of the year, it appears that periods of resource stress were common, especially during droughts. Although there are no direct observations of the study area itself during these periods, historical material in Reuther (1981) provides information on strategies used by Aboriginal communities in the north-east of South Australia generally, to deal with the major fluctuations in environmental conditions characteristic of the region.

Reuther noted that when resources were abundant, for example in periods after rain, communities utilised natural surpluses in a variety of ways. Large gatherings were organised to take advantage of the abundance of food and these aggregations had the primary function of satisfying social obligations through, for example, trade and exchange (1981: vol. 1: 42, 47–48). As well as these activities, people harvested more than they needed for immediate consumption, processing and storing the surplus for later use. Seeds, fish and grubs were the resources most favoured for this type of processing (1981: vol. 1: 13, 47–48, 232, 273, 491; vol. 2: 547, 772, 835, 915, 927; vol. 4: 1852; vol. 7: 458, 549, 659).

As well as these measures to maximise the

productivity of a region, according to Reuther the distribution of food resources was also artificially managed. He recorded that rats and caterpillars were moved from one area to another so as to increase stocks in particular regions (1981: vol. 2: 811–812; vol. 9: 232). Plant foods were propagated through the broadcasting of seed and the distribution of the branches of a particular vine species (1981: vol. 1: 107; vol. 7: 450). Areas of stream channels were dammed to increase stocks of fish (1981: vol. 8: 23). As well, certain localities were not utilised and were left in reserve for use during lean times, access to especially productive areas was strictly controlled and the boundaries of group territories were rigorously enforced (1981: vol. 1: 101, 123–128, 412; vol. 2: 559, 751, 1044; vol. 3: 1255, 1259). Transgressions, such as cases of people trying to obtain more food resources than their due, or attempting to accumulate resources, were severely punished according to Reuther, even by death (1981: vol. 1: 12–13, 123–129; vol. 2: 793–794). Further, instances were recorded of particular groups attempting to appropriate others' territory, sometimes successfully (1981 vol.1: 415; vol. 2: 896).

During times of drought people fell back to those areas which had water, and fish and stored food resources were the main foods consumed (1981 vol. 1: 520; vol. 2: 547, 616, 758, 915, 950; vol. 2: 1259; vol. 4: 1740). Although Reuther doesn't specify these areas, it is likely that the Coongie system and the Cooper channel near Innamincka were used in this manner.

Despite measures to counteract the effects of drought or a lack of surface water, local groups still suffered considerable stress. Reuther noted that many people perished at these times, from thirst, heat exhaustion or starvation (1981: vol. 1: 424, 535; vol. 2: 994–995, 1036; vol. 4: 1741–1742, 1926, 2108; vol. 8: 75, 118).

FACTORS OTHER THAN FOOD RESOURCES AFFECTING SETTLEMENT

It is a truism to state that it is not only the acquisition of food resources which affects the choice and nature of settlements. Access to raw materials necessary for the manufacture of goods and for trade, such as stone, wood, ochre, resin, bone, shell and the narcotic pituri, was another important determinant.

Historical accounts show that the Innamincka region was an important centre both for the

production of technological items, especially stone artefacts and for a related reason, as a crucial node in the vast exchange network which spanned the continent (Kerwin and Breen 1981: 286 and McBryde 1987). Innamincka was especially renowned for its extensive grindstone quarries (see Reuther 1981 vol.2: 899-900, McBryde 1987). The quarries, other important sites involved in the extraction of resources and the manufacture of goods, and the exchange networks of the Lake Eyre Basin generally, are currently being studied by McBryde and are thus not reported on here.

Although factors such as the utilisation of items for artefact manufacture and the location of trade and exchange networks are, as outlined above, crucial factors involved in settlement, not all of these features are equally archaeologically visible. For this reason I have chosen to look at one aspect that is more archaeologically visible than others, namely the characteristics of stone artefacts on lake-side sites and what these data, and other characteristics of the sites themselves, can tell us about Aboriginal use of the region. As outlined, stone suitable for the manufacture of artefacts is not uniformly distributed across the region and with the exception of Innamincka, stone sources and water sources do not generally coincide.

Two main sources of stone are present in the study area. Silcrete, chert and chalcedony are found as smallish pebbles on the surface of gibber plains, while better quality and more extensive areas of hard rock, comprising outcrops of chert, chalcedony, silcrete, quartzite and sandstone are found within the geological features known as the Innamincka and Cordillo domes (South Australia Department of Mines and Energy staff: pers. comm. and personal observation). Discrete areas of outcropping hard rock also occur within the linear dunefield south of the Cooper channel and east of Strzelecki creek (see Smith, Williams and Wasson 1991: 185).

Although there are no historical accounts of how Aboriginal people in the region quarried and used stone, apart from Reuther's observations on the Innamincka grindstone quarries, field observations and geological data can be used to determine what may have been favoured sources. It appears that while gibber pebbles were utilised, this took place on a relatively limited basis compared to other sources because of the relatively small size of the nodules of stone that could be worked. Outcropping areas of hard rock were thus favoured over gibber pebbles because they provided larger fragments of stone and were

more uniform in quality. As well, certain types of stone such as sandstone were not available as pebbles and were only located within hard rock localities.

Using data from geological mapping of the region and advice from South Australian Department of Mines and Energy staff, it is estimated that the Coongie system lies at least 60 km from good quality stone sources while the Cordillo lakes lie at least 20 km distant. Particular stone sources which would have been favoured include: the silcrete (including chalcedony, cherts, cherty silcretes and quartzites) of the Cordillo surface which caps the mesas and cuestas of the Cordillo and Innamincka regions and also includes the silicified Eyre formation and the silicified Winton formation; the Eyre formation which includes sandstones suitable for grindstone manufacture, and also small pebbles of agate and fossil wood, and the Cadelga limestone which includes a cherty limestone.

Surrounding these outcrops of hard rock and extending outwards for five kilometres or so are areas of gibber containing pebbles and larger blocks of stone eroded from these formations. Some of this material would have been utilised as well.

A MODEL FOR ARCHAEOLOGICAL SITE DISTRIBUTION WITHIN THE LAKE SYSTEMS

Historical observations can be combined with information on the availability of stone to present a model of how the lake systems were utilised. The model makes a number of assumptions, namely that there is a relationship between the availability of water and food resources; and intensity of occupation as reflected by the size and nature of archaeological sites. Cutting across these factors are others relating to the availability of stone, the most common material found on sites. Using models developed by other researchers such as Hiscock (1987), it is hypothesised that there will be a general correspondence between the morphology of artefacts on a site and distance from the stone source. These models predict that as one moves significant distances from stone sources, characteristics of extreme reduction of stone material will be found in assemblages such as recycling, rejuvenation and rationing. Combining these different models, we can develop a unified set of hypotheses regarding the patterning of archaeological material.

The Coongie system

The Coongie lakes, with their abundance of food sources, and availability of water for at least part of the year, were areas with a high population density relative to other lakes in the region. Large and diverse occupation sites will be found in those areas which contain the most predictable and extensive areas of water. Such places include the permanent waterholes on the channels, the inlets to lakes, and those parts of the lakes that are deeper relative to the rest of the lake basin and thus hold water for a longer period of time. These latter areas are found on the southern margin, since as outlined above, the lakes in the region are slowly migrating southwards, cutting into longitudinal dunes on their southern shore. Their southern end is thus their deepest section.

It is anticipated that given the known high population densities of at least the recent past, there will be a correspondingly high density of archaeological material (especially stone artefacts) on the large, favoured occupation sites. It is likely that on these sites people would not have moved as much compared to areas which contained less predictable resources. We can therefore expect evidence for the manufacturing and maintenance of tools such as stone artefacts. Given that the sites were used on a longer-term basis we can also expect a higher proportion of formal tool types than on sites with more unreliable water sources, and a greater proportion of finer-grained, good quality stone. As well, it is likely that a relatively larger number of artefacts will have edge damage from activities such as trampling, because of high population densities at the sites and residential stability (Scott Mitchell pers comm).

Because it is possible that people from other areas may have been using these localities as refuges in times of resource stress, it is also expected that these places will contain a wider range of raw material than at other sites, including stone brought in from other regions. Because stone sources lay some considerable distance away (60+ km), primary reduction was unlikely to have been undertaken here and the stone may have been 'rationed'. Cortex, an indication of primary reduction, will be rare on pieces. Flakes and cores will be small in size and noticeably reduced. High population densities and length of site occupation may have exacerbated the incidence of rationing, so that these features will be particularly marked at the

large sites near permanent or semi-permanent water.

The salt lakes

Given the absence of fresh water in these localities it is anticipated that they were not favoured as occupation sites. In times of high local rainfall it is possible that the lakes may have filled to some extent with rainwater run-off from the surrounding dunes. At these times salt levels may have decreased and they might have been used on a temporary basis as people pushed out into the dunefields after rain.

The salt lakes may have had another role, as navigation aids for people travelling through the dunefield. They are often the only notable features present within extensive areas of dunes and are visible for some distance because of the sun sparkling on the salt surface.

I conclude that the sites were used, albeit on a much more limited basis than the Coongie and Cordillo system. It is likely that groups using them were small in size and highly mobile. There is likely to be a correspondingly low density of artefacts, relative absence of formal tools, a more limited range of raw material types present and a lower proportion of good quality fine-grained raw material on occupation sites. Little manufacture or maintenance of artefacts will have been carried out on site. Given that the lakes are often well within the dunefield and thus some distance from stone sources, the stone discarded here will have been noticeably reduced.

The Cordillo lakes

With their better resources than the salt lakes the Cordillo lakes are likely to have been the subject of more intensive occupation but on a less pronounced basis than the better-watered Coongie system. It is anticipated that sites will be smaller in size than in the Coongie and fewer artefacts will be present. Because people occupied these sites for shorter periods of time it is expected that there will be less evidence for the manufacturing and maintenance of stone artefacts. A lower number and a smaller range of formal tool types will be present, and there will be less variation in raw material type. Larger sites are more likely to be located in areas of more predictable water and food resources such as the inlets to lakes or the small waterholes on channels.

Given that the Cordillo lakes are closer to raw material sources than the Coongie it is expected that stone artefacts will not be reduced as much. Cores will be more common and cores and flakes

will be heavier and larger in size, on average. A higher proportion of flaked pieces will contain cortex.

THE ARCHAEOLOGICAL SURVEYS: GENERAL ARCHAEOLOGICAL FEATURES OF THE LAKE SYSTEMS

Before presenting material on the archaeological sites examined as part of the study I will outline some of the factors affecting the location and recording of archaeological material in the field.

The visibility of archaeological material, especially stone artefacts, is reasonable compared to many other areas. The aridity of the region means that dense vegetation is often absent and much of the ground surface is exposed. This also means that stone sources are relatively straightforward to detect. Open sites are the major archaeological site type in the region because rock formations which form rock shelter sites are extremely rare here. Only one shelter (a very small and shallow one located near Innamincka) is known for the whole region. Although open sites are the major site type available for analysis, given the good ground surface visibility this is not necessarily the problem that it is in other regions. Stratified sites are extremely rare nevertheless and it is often very difficult to determine whether archaeological material is unequivocally in-situ, has been deflated down from other units, or otherwise re-deposited.

I will present general features of the archaeology of the lake systems first and compare them with my model. In the following sections I will discuss more detailed analyses of assemblages from a sample of collected sites so as to make a comparison between localities within the region.

The Coongie system

The results of this work are presented in Williams (1988) and are briefly summarised here, along with other material from 1987 surveys. Before outlining this information it is noted that not all of the lakes in the Coongie system were surveyed for archaeological sites. Coongie itself was not examined because it was already being systematically surveyed by a team of archaeologists from the South Australian Aboriginal Heritage Branch, (now within the Department of State Aboriginal Affairs), in relation to the development of a management plan for the region. The results of that study are not yet

available for analysis. Lake Goyder was not examined because in the years which formed the subject of my fieldwork (1986–1987) the lake was flooding out and thus conditions were not conducive to archaeological survey.

The most common site type around the lakes surveyed for the study comprised scatters of stone artefacts. In all sites surveyed these scatters were either located within upper recent sediments or appeared to have deflated down from such units to sit as a lag on more compacted surfaces. On many of the sites, scatters of freshwater mussel shell were also present. Although not all the margins of every lake were examined, it appeared that stone and shell was present as an intermittent scatter intermittently around the margins of lakes that were surveyed (Toontoowaranic, Marroocutchanie). These were often present as small scatters of shell with numbers of artefacts, similar to Meehan's (1982) 'dinnertime camps'. Artefact density and site size increased as one approached permanent water sources and the largest sites were found in the areas outlined earlier – permanent waterholes on the channels, the inlets to lakes, and the deeper, southern margins of the lakes. These latter sites often incorporated extensive scatters of shell as well. Compared to the large sites, site size and density of material was comparatively low on the pale-coloured transverse dunes. On these sites stone artefacts and scattered termite mound hearth fragments were the most common form of material.

Typologically, most, if not all artefacts dated to the mid to late Holocene. The main types noted were tula adzes and adze slugs, points, backed blades, small scrapers, cores, flakes and fragments of large, flat grindstones of the type described by Smith (1986). As well, single examples of large, cube-shaped silcrete cobbles which were commonly ground on one or more surfaces and in some cases also had flakes removed from edges and had thus been used as large cores, were often also present. Raw materials favoured for artefact manufacture were chalcedony, chert, cherty silcrete, a coarser-grained silcrete, and quartzite.

Other artefacts such as edge-ground axes and flaked pieces of quartz crystal were also found but appeared to be restricted in distribution to the lakes most difficult to access by vehicle. It appears that such artefacts were formerly present on other lake-side sites but, together with other types of artefacts such as complete grindstones, have been removed by collectors (a conclusion supported by oral tradition in the region and also personal

observation of collections held by individuals resident in the region).

Apart from the occasional large silcrete cobbles and remaining grindstones left on sites, stone artefacts were mostly small in size and appeared to be noticeably reduced. As well, although density of stone material varied with location, even on sites with comparatively higher numbers of artefacts, density was still relatively low compared to artefact scatters found in many other parts of the continent. On the larger sites average density for collected sites was of the order of 6–8 artefacts/square metre while on the smaller sites maximum densities were only 2–4 artefacts/square metre.

Occasionally larger flakes and horsehoof cores were found on sites or located as isolated finds within the dunefield or near lakes. There appeared to be no consistency in their location though and these were often in association with artefacts that typologically dated to the mid to late Holocene. As well, they were not noticeably patinated or weathered, and did not appear to be derived from Pleistocene sedimentary contexts, suggesting that most of these are mid to late Holocene in age.

Hearth material, usually fragments of burnt termite mound, was often scattered across sites and isolated hearths were also present. The amount of hearth material rose in density on the larger sites and on these latter places fragments of bone (mostly that of fish and small mammals) were often found as well. The large sites are indeed extensive – examples up to 10 000 square metres and 7 000 square metres in extent respectively are described in Williams (1988: 59).

Dating of material on sites confirms that implied by the typology of artefacts, that is, of the late Holocene. Details of radiocarbon dates are provided in Williams (1988).

The archaeological data is consistent with the ethnographic observations that the Coongie lake system was extensively used and densely populated. The presence of good quality raw material and a range of artefact types, including formal tools and manufacturing debris, suggests that residential stability could have been fairly high in comparison to other areas. This is also supported by the wide range of archaeological material present, including bone and shell. The small size and marked reduction of artefacts indicates rationing of raw material was taking place and this is consistent with the distance of the area from stone sources.

The salt lakes

As expected, within the areas sampled for sites

for Coorie Coorie Tillie and Lake Deception, archaeological material existed in very low densities. At Coorie Coorie Tillie for example, along the 5 km stretch of the transverse dune on the northern margin of the lake only five isolated artefacts were seen: three amorphous flakes, one tula slug and one small corc. All artefacts were manufactured from silcrete. Archaeological material was similarly rare at Lake Deception. Sites comprising occasional small, discrete groups of artefacts were found in the vicinity of both lakes but not within the transverse dune systems. Instead they were set back one or two longitudinal dunes from the lake margin, on the surfaces of small claypans.

The sites found in these areas comprised small (mostly less than 30 artefacts), discrete scatters of stone artefacts. Density was very low, much less than 1 artefact/square metre. Neither mussel shell nor animal bone was present on these sites or on other parts of lake margins but occasionally examples of isolated termite mound hearths were found in association with the stone artefact scatters.

One of the termite mound hearths at Coorie Coorie Tillie was dated. To examine particular features of the region's environment which may be affecting dates, the material was separated into a humic and non-humic fraction and each sample separately dated. The humic fraction returned a date of 1150 ± 180 BP (ANU 6181) and the non-humic: 710 ± 170 BP (also ANU 6181). The disparity in the dates can be explained as follows. John Head, ANU Radiocarbon Laboratory, confirms that the non-humic fraction, comprising clay particles, binds to younger carbon and clay material, biasing the date and making it too young. To account for this the non-humic fraction, which although comprising polymers which can incorporate younger carbon, was treated with solvents so as to extract the older carbon which is more likely to be reflecting the true age of the sample (pers. comm.). The older carbon is dated and the result, 1150 ± 180 BP, is the best estimate of the sample's true age.

Apart from the differences in density and site composition from the Coongie sites, other distinguishing features were also apparent. Most of the artefacts were manufactured from a relatively restricted range of raw material, assemblages being dominated by a grey, comparatively coarse-grained silcrete. Some cores were present and also occasional formal tool types such as tulas, scrapers or points. Artefacts appeared to be noticeably larger than those at

Coongie. Because of the low density of material, and also given the difficulty of access to the sites, collections of artefacts were not made when the sites were visited and so a more formal comparison between these features and other lake systems is not possible. The low density of material present on these lakes suggests that while they were utilised, they were not favoured for occupation. The restricted range of raw material found, its contrast in quality to the fine-grained material found on the Coongie system and the relative absence of manufacturing debris, indicates people used these areas on an opportunistic basis. The low numbers of artefacts present also suggests that group sizes were relatively low.

The Cordillo lakes

Vehicular access to the lakes was difficult because of their remote location and thus only one lake, Koonoomoorinna, was surveyed in detail. Reconnaissance trips to other lakes in the region revealed that the general patterning of sites on this lake is similar to that on others.

As for other parts of the study region, the most common site types seen were scatters of stone artefacts. Formal tool types were similar to those observed on the Coongie sites, comprising tulas and other adzes, scrapers, points, fragments of grindstones and the large silcrete cobbles with ground and/or flaked surfaces. Formal types did not appear to be as common within assemblages as for the Coongie and no shell or bone was present on sites. The range of raw material did not seem as extensive and finer grained raw material such as chert and chalcedony was found in lower densities. Artefacts appeared to be larger in size and not as heavily reduced.

Hearths were also not as common and no hearth sites were observed on any of the sites ringing the immediate margin of the lake. A small number of hearths were found in the inter-dune corridors one or more dunes back from the lake margin. One, comprising burnt calcrete nodules, was dated and returned a 'modern' radiocarbon age (100.2, 1.8 %M, ANU 6183), although this sample may have been contaminated by younger carbon from the surrounding locality (John Head pers. comm.).

The densest, most extensive scatters of artefacts were found in those areas with the most reliable sources of water – inlets, the southern margin of lakes, and on the edges of possibly semi-permanent waterholes along the channels which connect the lakes. A large scatter along one of the channel waterholes contained a number of hearths. Intermittent, low density scatters of artefacts were

found along the lake margins and on the transverse dunes to the north.

The archaeological patterning is consistent with the hypothesis that the Cordillo lakes were utilised more than the salt lakes but less than the better-watered Coongie area. This is supported by the fact that the Cordillo sites contained a smaller range of archaeological material than the Coongie sites (no shell or bone, hearths not as common, a lower density of formal tool types and of better quality stone). The relative lack of reduction of artefacts could indicate either less residential stability or a closer distance than Coongie to raw material sources, or both.

Now that I have presented general observations of the archaeology of the lake systems I will outline the results of the more detailed comparisons between sites. This work provides a more fine-grained analysis of differences that may exist across lake systems and between systems.

MORE DETAILED COMPARISON OF ASSEMBLAGES FROM INDIVIDUAL SITES

Because of the relatively low density of artefactual material within the region, for reasons of statistical analysis I only made formal collections from large sites. The sites analysed in this way are outlined below, along with the results of the analysis.

Before discussing the sites it is noted that although some of the analysis of the material was published in a preliminary form by Smith, Williams and Wasson (1991, see for example Tables 11 and 12), a number of the figures in that paper vary slightly from those presented in this publication. This is due to the fact that the results of the analysis of the Coongie sites outlined in the 1991 paper were only at a preliminary stage. The material presented in the current paper reflects the completed analysis of the assemblages.

Sites chosen for analysis

Five sites were chosen for analysis: Marroocoolcannie 2 (MCO 2), Toontoowaranie 1 (TTW 1), Lake Lady Blanche midden (LLB), Koonoomoorinna inlet (KOI) and Koonoomoorinna second white transverse dune (KSW). The first three sites are located on Coongie lakes – their name indicates on which lake they are situated, and the latter two sites are located on the southern-most of the Cordillo lakes, Koonoomoorinna. All sites comprise large, discrete scatters of stone artefacts, together with

other material such as shell and bone in some cases.

The lakes were chosen for sampling and analysis to determine whether there were any major changes in stone artefact manufacture and discard across the Coongie system. Each site was chosen because it was the most extensive seen for the sampled areas of that particular lake. MCO 2 lies along the western margin of the channel feeding from Lake Marroolcoocannie to Lake Marroocutchanie. It covers an area of approximately 2 600 square metres and comprises a scatter of artefacts and shell deflating down from the uppermost recent unit of a pale, longitudinal dune. The material exists as a lag on a blow-out within the dune. At the western end of the site is a localised area of burnt shell and bone, the latter comprising the remains of fish and small mammal species. A hearth, which lies on the eastern part of the site, dated to 1130 ± 110 BP (ANU 429).

A baseline was laid through the middle of the scatter so as to bisect both the area of burnt bone and the hearth. All artefacts along a strip 60 m along the baseline and 1 m either side of it were collected for analysis.

TTW 1 lies further to the north than MCO 2, located on the southern margin of Lake Toontoowaranie. It covers an area of 7000 square metres and comprises stone artefacts, shell and the remains of the collapsed, wooden framework of a domed hut, all lying on recent sediments on the top of a longitudinal dune. A sample of shell from the site returned a date of 330 ± 80 BP (ANU 5425). A 20 x 2 metre grid was laid out within the centre of the scatter and all artefacts within this were collected.

LLB lies to the north and west of MCO 2 and TTW 1, on the inlet channel to Lake Lady Blanche, one of the terminal lakes in the Coongie system along with Lake Sir Richard. These two lakes hold water for a shorter period of time than those closer to the North-West Branch. When the lake was visited in August 1987 it was dry and had a salt crust on the lake floor. This was in contrast to the other Coongie lakes which were all full of water.

The site comprises a large scatter of stone artefacts, shell and bone extending for 12 000 square metres, eroding out of the uppermost units of a recent, white transverse dune associated with the inlet channel and flood-out zone of the lake. The bone comprises fish bone and golden perch otoliths. It is the largest and richest site in the inlet area. A 15 x 15 metre grid was laid out on the eastern edge of the exposure, where the

densest scatter of shells, otoliths and artefacts was eroding out of the sand. All artefacts within the grid were collected.

The relative lack of water in the lake compared to others in the Coongie system reflects the distribution of sites in the area. Large sites such as this one, which are not only extensive but contain a variety of material, are restricted to the margins of the inlet channel. Isolated scatters of stone artefacts are found on the surface of the complex of at least five separate transverse dunes lying to the north-east of the lake, but these sites are small, discrete scatters of stone artefacts and do not contain shell, bone or hearth material.

Although the lake contains water on fewer occasions than others in the system, it was much favoured by Aboriginal occupants. McKinlay visited the lake in January 1862 and found it full of water, 'between five and six feet deep, and seven and three quarter miles in circumference ... and tens of thousands of pelicans on it ... with innumerable other birds ... and plenty of fish' (1862: 38). There was a large camp of at least 150 people on the lake when McKinlay was there and he observed that fish and 'nardoo' was their chief sustenance (1862: 42).

For the Cordillo lake, Koonoomoorinna, two areas were sampled for artefacts. Both sites, KOI and KSW were the most extensive discrete scatters of artefacts seen within the vicinity of the lake and this is why they were chosen for analysis.

KOI is a very extensive scatter of artefacts which follows the inlet to Lake Koonoomoorinna for several hundred metres. The site comprised stone artefacts only – no shell, hearths or bone were present. A small part of the site (10 m by 2 m) where the densest collection of artefacts was found, was gridded and a collection made.

KSW comprises a discrete scatter of artefacts lying as a lag within a blow-out in the second transverse dune north of the lake. Like KOI, only stone artefacts were present within the site.

MCO 2 and TTW 1 lie 65 km from sources of outcropping hard rock in the Innamincka dome and 60 km from the Cordillo dome sources. LLB lies 40 km from the Cordillo dome sources and 65 km from the Innamincka dome. KOI and KSW lie 30 km from the Cordillo dome and 90 km from the Innamincka dome.

For comparative purposes, the five lake-shore sites are compared with each other and also with one from the waterless core of the dunefield, site JSN. This latter site, which is reported on in Smith, Williams and Wasson (1991), comprises a scatter of stone artefacts and hearth material, and

Table 1. Characteristics of artefacts within assemblages, excluding ground pieces

Site	mean weight in gm, (sd)	% flakes	% cores	% formal tool types
KSW n=291	7.55 (17.57)	70.4	3.4	3.8
KOI n=308	5.14 (20.53)	48.4	4.2	2.6
LLB n=336	2.65 (7.11)	45.2	0.6	11.9
TTW 1 n=264	1.74 (3.33)	59.5	—	4.2
MCO 2 n=661	2.17 (8.32)	50.1	0.6	5.6
JSN n=407	6.6 (sd not available)	37.3	2.7	not available

is the only known Pleistocene site in the region. Hearths from the locality date to around 14 000, 10 000 and 2 500 BP. Associated with the hearths and lying as a lag on two inter-dune pans within longitudinal dunes is an extensive scatter of artefacts. Despite the Pleistocene dates for the hearths, analysis of the stone artefacts strongly suggests that they are late Holocene in age (Smith, Williams and Wasson 1991: 184).

JSN was chosen as a comparative site for the lakeside sites because it comprises the only known extensive scatter of stone artefacts for the core dunefield region. Most core dunefield sites only consist of an isolated artefact or very small scatters of stone artefacts (personal observation). The large size of the artefact sample ($N = 407$) from JSN and the fact that the artefacts appear to be late Holocene in age, similar in age to the lakeside sites, makes it the only comparative material currently available for the Coongie and Cordillo sites.

Table 2. Values of t for comparison between mean weights of artefacts

Site	KSW	KOI	LLB	TTW 1	MCO 2
KSW	—	—	—	—	—
KOI	not significant	—	—	—	—
LLB	$t = 4.71$	$t = 2.11$	—	—	—
TTW 1	$t = 5.33$	$t = 2.72$	not significant	—	—
MCO 2	$t = 6.48$	$t = 3.22$	not significant	not significant	—

Table 3. Mean weights of cores (gm)

Site	n	mean	sd
KSW	10	58.29	50.49
KOI	13	42.62	81.75
LLB	2	13.7	1.90
TTW 1	—	—	—
MCO 2	4	7.65	6.56
JSN	12	89.2	57.9

Table 4. Percentage of artefacts larger than 1 cm in length which contain cortex.

Site	% artefacts with cortex
KSW	12.4
KOI	11.0
LLB	4.29
TTW 1	9.2
MCO 2	3.2
JSN	20.0

Analysis of the sites

Broad characteristics of the stone artefact assemblages are presented in Table 1. As predicted by the model, the Coongie assemblages have features reflecting an extreme degree of reduction. Artefacts (all pieces of stone on the site worked in some way, excluding ground pieces) are extremely small in size (measured by mean weight in grams) and cores are very rare, or even non-existent in the case of TTW 1. The Coongie sites are very similar to each other but are different to both the Cordillo sites and JSN, which contain larger artefacts and a greater number of cores respectively.

The differences in mean weight between the

Table 5. Raw material composition of the assemblages (excluding small shatter < 1cm in length and including ground pieces)

Site	% Finer grained	% Coarser grained	% Very coarse grained (eg sandstone)
KSW (n=278)	47.1	41.7	11.2
KOI (n=239)	37.2	59.0	3.8
LLB (n=223)	72.6	19.3	8.1
TTW 1 (n=223)	66.4	27.4	6.3
MCO 2 (n=659)	59.8	23.7	16.5
JSN (n=401)	59.5	33.2	7.4

Table 6. Mean weights and mean lengths of complete flakes for different raw material types. Standard deviations are shown in brackets. Note: Only those artefacts > 1 cm in length have been included in this analysis because of the difficulty in determining whether smaller pieces were derived from finer or coarser-grained raw material. Ground pieces and sandstone have also been excluded from the sample.

Site	mean weight (gm) of complete flakes		mean weight (gm) of debitage >1 cm in length		Mean length (mm) of complete flakes	
	finer grained	coarser grained	finer grained	coarser grained	finer grained	coarser grained
KSW	3.9 (4.1)	12.0 (18.6)	3.2 (2.7)	7.4 (14.1)	25.0 (9.4)	31.7 (13.6)
KOI	2.3 (2.6)	6.71 (15.6)	2.3 (2.9)	5.0 (7.1)	17.8 (7.1)	25.2 (14.60)
LLB	1.3 (2.0)	2.1 (2.8)	3.1 (4.6)	9.3 (21.8)	15.8 (5.1)	19.1 (6.8)
TTW 1	0.9 (1.1)	4.8 (6.4)	1.0 (1.7)	7.4 (14.9)	15.8 (6.1)	26.3 (14.7)
MCO 2	0.9 (1.5)	8.0 (24.3)	0.9 (0.9)	3.5 (5.3)	15.2 (5.3)	23.5 (16.2)
JSN	3.1 (3.2)	4.7 (10.6)	5.6 (13.0)	3.5 (6.4)	not available	

Coongie and Cordillo assemblages are significant at the 0.05 level (Table 2). The figures for JSN are not available for comparison but it is anticipated that if they had been available, the mean weight of the assemblage would be statistically different to the Coongie sites but of the same order as the Cordillo assemblages.

As predicted by the model, the three groups of sites are very different in relation to the reduction of cores (Table 3). The cores from the Coongie sites are extremely small and, as outlined in Smith, Williams and Wasson (1991:187), very close to the theoretical limit at which bipolar techniques become necessary for further reduction. Consistent with this is the observation that in a further attempt to ration raw material, worked-out or small, broken cores have been recycled into small scrapers in the Coongie assemblages ($N=9$, mean weight = 8.2 gm, $sd = 4.9$). The Cordillo sites contain cores that are noticeably larger and heavier than those on the Coongie sites, while JSN contains on average larger cores again. There is no evidence that cores have been recycled as implements at either the Cordillo sites or at JSN.

The Cordillo sites contain proportionately greater number of flaked pieces with cortex than Coongie (Table 4), which is as predicted given that they lie closer to raw material sources, although the figures for TTW seem high in comparison to the other Coongie sites. The JSN assemblage contains an unusually high number of flakes with some degree of cortex. This feature is unexpected and as well as the relatively larger size of cores and flakes, indicates that the JSN assemblage shows neither the effect of relatively large distance from stone sources, nor mediating

responses offsetting a diminishing stock of stone (see Smith, Williams and Wasson 1991: 187). This issue is discussed in more detail later in this paper.

Regarding raw material composition for assemblages, Table 5 shows that the Coongie sites contain proportionately more finer grained material (classified here as chalcedony, chert and cherty silcrete) than either the Cordillo sites or JSN and this is as expected (coarser-grained material has been classified here as granular silcrete and quartzite). Table 6 shows that flakes and debitage from fine-grained material are on average smaller in size and lighter in weight than those from coarser-grained material, but this does not explain all the variation in size between assemblages between sites in different areas. Fine-grained flakes and debitage from the Coongie sites are in virtually every case smaller in size and lighter in weight than fine-grained pieces from either the Cordillo sites or JSN.

As well as these trends, the Coongie sites also show a wider range of raw materials as predicted. MCO 2 has 13 major types of raw material, TTW 1 has eight types, LLB has seven, KOI has five and KSW has seven.

In terms of the artefact analysis it was decided not to differentiate artefacts with retouch from those where this feature appeared to be absent. This is because of the difficulty found in unambiguously identifying examples of retouched pieces within the Coongie and Cordillo assemblages. Numbers of artefacts within the assemblages contained what I recorded in my analysis as 'edge damage', where I describe this as an edge where very small flakes had been

removed and there is also a gloss or polish (visible under low-power magnification). However given the small size and thin cross-section of many of the flaked pieces it was impossible to determine whether this edge damage had occurred as a result of use, or as deliberate retouch, or from some other process such as flaking or trampling for example. Accordingly it was not possible to examine one of my hypotheses, that sites near more permanent water sources would show more edge damage from trampling.

Because of the difficulties in identifying what had caused the edge damage, none of the statistics for this feature have therefore been listed for this analysis. It is noted that in the assemblages examined there were very few artefacts with pronounced retouch (where this involved larger flakes being removed along an edge and/or very obvious polish) which did not also comprise a formal tool type such as a scraper, adze, point or backed blade. For the very few artefacts which did not fit in to a formal category they were nonetheless listed under 'formal types' in my tables.

Given that this classification methodology differed from that used for the JSN artefacts, it has not been possible to compare the two groups in a formal sense. Nonetheless some comparison are possible.

In terms of my category of 'formal tool types', the Coongie sites contain a greater proportion of these artefacts than the Cordillo sites (Table 1), as predicted. Adzes such as tulas and tula slugs formed the largest proportion of formal types in the Coongie sites (59% for MCO 2, 45% for TTW 1 and 55% for LLB). The remaining implement types comprised scrapers, points and backed flakes. For the Cordillo sites in contrast there is greater variation in the formal types of stone tools represented on sites. Adzes comprised 36% of the formal types present at KOI but only 18% of those at KSW. At KOI scrapers comprise the most common formal type (50%) while at KSW, points, backed flakes and backed blades are the most common type at 64%.

Regarding the artefacts comprising formal types, it was expected that examples will be more heavily reduced at sites near permanent water. Examining the largest sample of a formal type available, tula adzes and tula adze slugs, it is found that this is not the case. There is no clear trend in mean weights between the Coongie sites (MCO 2: mean = 8.5 gm, sd = 5.02, n = 15; TTW 1: mean = 3.25 gm, sd = 1.35, n = 2; LLB: mean = 14.18 gm, sd = 10.1, n = 19) or between

the Coongie and Cordillo sites (KOI: mean = 3.7, sd = 1.0, n = 2; KSW: mean = 6.8, sd = 2.7, n = 2).

This suggests a number of factors. While overall characteristics of the assemblages presented in Table 1 show that stone was being curated and rationed in a very intensive way for the Coongie sites, the variability in size at discard for tulas and tula slugs, especially the relatively higher weights for the LLB site, suggest that occasionally the site occupants were not behaving as if raw material was as scarce as it appeared to be. This suggests that while certain factors such as the balancing of procurement of food and water sources with that of raw material is responsible for much of the variation seen on sites, people did not always behave as if this was the only equation affecting the nature of occupation and discard of stone artefacts.

Although the JSN assemblage has been classified according to a different typology, a preliminary analysis of it reveals that formal types are rarer than at either the Coongie or Cordillo sites. This is consistent with the model. As well, it is further observed that adzes are not present on the site. A possible explanation for this relates to the lack of hardwood trees within the core dunefield region supplying suitable wood for adzing activities. The absence of such trees is very likely related to the availability of water – hardwood specimens being found on the banks of waterholes and lakes.

COMPARISON OF THE TRENDS IN THE ASSEMBLAGES WITH DATA FROM OTHER PARTS OF THE ARID ZONE

The trends seen in the assemblages for the region are also echoed in other arid zone work available for comparison. The major study which provides comparative data is that of Veth (1993) for the Western Desert region, Western Australia. His analysis shows similar patterning to that outlined above, with features of assemblages from sites at permanent waters indicating more intensive stone reduction than for either semi-permanent waters or ephemeral water sites. His data show that differences in intensity of reduction are not as clear between semi-permanent and ephemeral water sites as they are between these sites and more permanent ones (see 1993: Tables 8.21–8.31). For a number of features, ephemeral sites show trends characteristic of more intensive reduction than semi-permanent sites, which is not predicted by Veth's model. This appearance of

conflicting trends also appears to be echoed by comparisons between the Cordillo sites and JSN. The sites are more similar to each other than they are to the Coongie sites but there is much variation in the nature and direction of trends between the two groups. This suggests that the permanent sites, in Veth's sample and mine, form clear groups but other sites, while showing some similar trends, are more variable.

The association of higher proportions of formal types in assemblages, especially adzes, with more predictable water sources, is also a trend noted by Veth (1993: 95–96). Veth also found that there was some patterning in the amount of reduction of tula adzes and relation to water sources but that there was a considerable degree of variation (1993: 98–101) and this is also found in my samples.

In his discussion of his results of the artefact analysis, Veth concludes that the timing and intensity of site use are the major factors responsible for variation in the assemblages, rather than distance to raw material sources and the operation of specific discard criteria (1993: 101). This also seems to be the case for the north-east South Australian sites, as I will outline below.

MAJOR FACTORS AFFECTING THE PATTERNING OF SITES IN THE REGION

One of the predictions of my model of site patterning is that apart from water sources, availability of stone sources is one of the most important factors responsible for trends seen and that Aboriginal occupants favoured raw material sources closest to the site.

An examination of the JSN assemblage reveals that the people who visited the site did not behave in this manner. Rather than using the closest stone to the site (40–50 km to the east) for artefact manufacture and discard, the sourcing of stone artefacts from the site indicates that they instead used stone from Della-Dullingari which lies 115 km away, to the north-east (Smith, Williams and Wasson 1991: 185). Despite the use of such distant material, the assemblage does not have features characteristic of extreme reduction (Smith, Williams and Wasson 1991: 185–189). Cores have not been noticeably curated and have not been recycled as other implements. Mean weight of artefacts is significantly greater than for the Coongie sites, despite the fact that utilised stone sources are considerably further away than

for the Coongie. Flaked pieces contain much higher proportions of cortex, also consistent with less intense reduction.

The patterning of the JSN assemblage is characteristic of a situation where raw material is closer rather than further away. Yet the paradox can be resolved if we instead see stone source utilisation in terms of re-supply time rather than just in terms of linear distance of stone source from occupation site. For example, if people stopped at JSN as part of a journey to the Della-Dullingari region, they would have been aware that they were only a couple of days away from being able to replenish stone sources. As well, it is likely that the duration of visits to the JSN were relatively short, so that the demand for stone was easily met by the stock-in-hand without recourse to the recycling and the extreme reduction of stone evident at the Coongie sites (Smith, Williams and Wasson 1991: 188).

The JSN site shows that it is not necessarily linear distance from the closest stone sources that is a major factor in the patterning of stone artefact manufacture and discard. The key factors are instead the length of time spent at the site, which in turn relates to the length of time before the group could replenish stone sources.

This line of reasoning can be applied to the Coongie sites as well. The extreme reduction of stone reflected by the assemblages can be seen as the archaeological correlate of residential stability within the lake system relative to other environments in the region. It appears that people chose to stay closer to the lakes even if it meant that they were restricting their access to stone, thus triggering what appears to have been significant pressure on the way they used the resource. This is despite the fact that they could have chosen to be more mobile, travelling more often between stone sources and the lakes. In this latter case, features of such extreme reduction would not be visible in assemblages.

Therefore, like Veth for the Western Desert region, I see the main determinant of site patterning in the Coongie and surrounding areas as relating to the timing and intensity of site use rather than to distance from raw material as such.

This indication of relative residential stability in the Coongie, combined with the high population densities observed in the area at the time of contact implies that the system may have been vulnerable to significant stress given the extreme environmental fluctuations characteristic of the region. It is likely that the system worked

smoothly when resources were abundant but in cases when an anticipated flow of fresh water failed to come down the Cooper or when there was widespread drought, it is possible there were major problems. The fact that the current situation where the Coongie captures most, if not all of the Cooper flow, is potentially very unstable and channel flow could be completely switched on and off as a result of only slight environmental shifts, would exacerbate this.

Ethnographic observations support the notion that stresses were operating on the system. The rigid sanctions outlined earlier involving the enforcement of group boundaries and access to resources indicate this, along with the information that many people in what is now the north-east South Australian region perished during droughts. Further, Wasson's observation of a dune mobilisation event in the late Holocene that might be linked to the intensity of the occupation of the region, is another feature that suggests the system might have been under some stress.

Evidence for 'intensification'?

It is tempting to suggest that the characteristics of the mid-late Holocene occupation of the region reflect an intensive settlement pattern and are derived from a process of 'intensification' (see also Williams 1988: 61). For example, all of the dates for occupation sites for the Coongie system fall within the late Holocene and on all sites recorded within the region, including JSN, the typology of artefacts suggests a mid-late Holocene date. While it is tempting to conclude the region does provide evidence consistent with the operation of such a process, as in my 1988 paper I am cautious about maintaining that these features provide definite evidence. I take this position because it is likely that the environmental instability could be causing major biases in the archaeological record. Such instability could be selectively removing older sites from the archaeological record, or rendering them archaeologically invisible through sedimentation, or even resulting in vast fluctuations in channel flow thus affecting the filling of lakes. I therefore conclude that while the evidence for intensification is persuasive, further geomorphological work is needed to more fully expand on factors affecting the visibility of archaeological material.

Given these issues, can any conclusions be drawn about the occupation of the arid zone, especially that of the more distant past?

EARLY OCCUPATION OF THE ARID ZONE

I will conclude the paper with some brief and speculative comments about models relating to when the arid zone was first occupied on a consistent basis.

As noted in Smith, Williams and Wasson (1991: 190) the evidence from the JSN site indicates regular use of the dunefield region during the late Pleistocene, when there was probably also occupation of the riverine corridors. The presence of *Velesunio* shell at JSN in a Pleistocene context is tangible evidence of some link with these riverine habitats. The nature of the archaeological material present on the site suggests that late Pleistocene use did not involve much on-site stone working and that this changed some time during the mid-late Holocene when visits to the area appear to have become more prolonged and to have involved the grinding of seeds and the manufacture and maintenance of chipped stone artefacts (*ibid*).

Dating of hearths to the period around 12 000 BP for hearths on the lower reaches of Coopers Creek (Veth, Hamm and Lampert 1990) is also consistent with late Pleistocene occupation of what is now north-east South Australia.

Despite the presence of the dunefield site of JSN, Veth (1993) has developed a model suggesting that the continent's core arid zones were only colonised as recently as 5 000 years ago. Veth maintains that the evidence for Pleistocene occupation of JSN does not disprove his model since the Strzelecki dunefield region is located within an area of co-ordinated drainage, thus implying that it was not part of the core arid zone (1993: 111).

Veth's model is an interesting one, but it could prove difficult to test. His 'core arid zones' comprise the deserts of the Great Sandy Desert, Great Victoria and Simpson Deserts. These regions are by definition sandy deserts and are thus areas where outcrops of hard rock are rare and therefore rock shelters with potential Pleistocene sediments are either non-existent or uncommon. Rockshelters such as those examined by Veth (1993) in the Gibson Desert, have late Holocene occupation resting directly on bedrock and thus do not provide contexts for the examination of occupation (or the lack of it) for the period before the late Holocene.

The fact that the presence of rockshelter sites which preserve Pleistocene sediments is so crucial for the examination of whether Pleistocene occupation took place or not, is shown by Veth's

discussion of his model (1993: Chapter 9). All of the eleven Pleistocene sites and early Holocene sites which lie a considerable distance from co-ordinated drainage, and thus form the basis of his model, are rockshelters.

Knowing that rockshelter sites which preserve Pleistocene sediments are likely to be extremely rare in the regions important for Veth's model, it is also unlikely that Pleistocene open sites will be easy to locate. Extensive outcrops of hard rock are not common in the sandy deserts and thus stone suitable for the manufacture of artefacts is also a scarce commodity. It is therefore likely that stone artefact manufacture, one of the major archaeological indicators of human occupation, has to take place on a relatively intensive basis before it becomes archaeologically visible in these regions. The JSN site for example indicates that Pleistocene occupation is not as archaeologically visible as regards stone artefact discard as is mid-late Holocene occupation. This evidence is complemented by my findings for the study area that artefacts do not appear to be present within visible Pleistocene contexts. This is despite that fact that we know from the evidence of JSN that people were using the region during the late Pleistocene.

Further, the logistical difficulties of carrying out systematic archaeological surveys for sites in remote locations such as sandy deserts, compound these problems. JSN was not found as the result of systematic archaeological sampling but was instead located virtually by accident during the course of a geomorphological study of the dunefield by Wasson.

The question of when the core arid zones were first occupied on a systematic basis thus remains a challenging one. Until this question is resolved, JSN remains the continent's sole example of a Pleistocene site located within the midst of the

continental dunefield, albeit a dunefield in the vicinity of co-ordinated drainage. The spur to the finding of Pleistocene sites within Veth's 'core arid zones' will be to expand further on the nature of the continent's Pleistocene occupation and to also determine the antecedents of the patterning seen in the mid-late Holocene.

ACKNOWLEDGMENTS

The project reported on in this paper was funded jointly by the National Research Fellowship Scheme and the Department of Prehistory, Research School of Pacific Studies, (now the Division of Archaeology and Natural History), the Australian National University. I thank these bodies for support. The Australian Heritage Commission also provided some assistance and I thank Betty Meehan particularly in this regard. Bob Wasson was instrumental in encouraging me to initiate the Coongie project and I especially thank him for his advice and support during the course of the work. SANTOS provided much logistical support for fieldwork and I particularly thank Oleg Morozow and Steve Tunstall for their assistance. The Aboriginal Heritage Branch gave permission for collection of sites and the excavation of JSN. Chris Dodd (then Aboriginal Liaison Officer, SA NPWS) gave approval for the excavation of JSN and I especially thank him for his assistance with work on the site. I wish to thank all of the people who provided assistance in the field: Doreen Bowdery, Nick Drayson, Ros Fraser, Parry Kostoglou, Gary Dunnett, Pam and Colin McDonald, Ben Smith, Barney Stevens, Steve Sutton, and Keryn Walsh. I am also indebted to Barry Saunders and Vince for their advice and support in the field, and the Royal Flying Doctor Service whose radio network was invaluable in such a remote area. I particularly thank my co-worker at JSN, Mike Smith; useful advice and discussion on ideas in this paper were provided by him, Bob Wasson and Barry Cundy. I am also especially grateful to Win Mumford for her work on the maps and illustrations.

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**REVISION OF AUSTRALIAN *AMPHIOPS* ERICHSON, *ALLOCOTOCERUS*
KRAATZ AND *REGIMBARTIA* ZAITZEV (COLEOPTERA: HYDROPHILIDAE)**

C. H. S. WATTS

Summary

The Australian members of the Hydrophilid genera *Amphiops* (five species), *Allocotocerus* (three species) and *Regimbartia* (one species) are revised and redescribed. Keys to species of *Amphiops* and *Allocotocerus* are given. *Amphiops austrinus*, *Amphiops micropunctatus* and *Allocotocerus yalumbaboothbyi* are described as new.

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Manuscript received 15 April 1997.

The three genera included in this revision are grouped for convenience not phylogeny although both *Allocotocerus* Kraatz, 1883 and *Regimbartia* Zaitzev, 1908 belong in the same tribe (Berosini) and they and *Amphiops* Erichson, 1843 are frequently mixed together in collections. All are wet-tropical beetles with, at the generic level, a wide distribution outside Australia (Hansen 1991). They are all relatively small very deep-bodied insects with *Amphiops* and *Allocotocerus* having almost spherical bodies. They occur commonly in pools and swamps around the tropical coast from the Kimberley to about Sydney.

The most recent taxonomic work on the Australian species was by J. Balfour-Browne who briefly commented on them and described *Allocotocerus tibialis* and *Amphiops queenslandicus* (Balfour-Browne 1939) and Hansen, 1991 who discussed their generic placement.

Material was examined from the following collections.

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection
BM(NH)	Natural History Museum, London
NMV	Museum of Victoria
NTM	Northern Territory Museum
QDPIM	Queensland Department of Primary Industries, Mareeba
QM	Queensland Museum, Brisbane
SAMA	South Australian Museum, Adelaide
UQIC	University of Queensland Insect Collection, Brisbane
WAM	Western Australian Museum, Perth.

SYSTEMATICS

The three genera can be separated from other Australian aquatic Hydrophilids by the following characters (after Hansen 1991).

Amphiops: Size 2.5–4.5 mm. Dark brown to black. Eyes divided into upper and lower portions by extensions of side of head. Elytra approximately as high as long, without striae. Meso- and meta-tibiae without swimming hairs. First ventrite very short, with a fringe of fine setae rising from its basal margin.

Allocotocerus: Size 3.5–4.5 mm. Black. Meso- and meta-tibiae with swimming hairs. Eyes normal. Elytra as high as long, virtually without striae.

Regimbartia: Size 3.5–5.0 mm. Black. Meso- and meta-tibiae with swimming hairs. Eyes normal. Elytra high, about 2.8x longer than height, with distinct striae.

For more detailed descriptions and discussion of the affinities of these genera see Hansen, 1991.

Amphiops Erichson, 1843

Australian *Amphiops* are all very similar and are best separated by the male genitalia. Indeed I have found it impossible to reliably separate *A. queenslandicus* J. Balfour-Browne and *A. duplopunctatus* Blackburn by any other means. The best general character is the form of the elytral punctuation, in particular the interstitial punctuation on the sides of the elytra. There are three more or less distinct size classes of elytral interstitial punctures: 1) large, about the size of the stria punctures; 2) small, between about 20–

60% of the larger ones; 3) micro, which are normally no more than pin pricks even under moderate magnification.

KEY TO AUSTRALIAN AMPHIOPS

- 1 — Interstitial punctures consisting of a few large punctures and a few to numerous micro punctures, the small size seemingly absent (Figs 1&3). Systematic punctures on pronotum large and distinct 2
 - Interstitial punctures consisting of large, small and micro punctures with small predominating (Figs 2 & 4). 3
- 2 — Central lobe of aedeagus not hooked (Fig. 13). First elytral stria (close to suture) distinct, traceable (anteriorly) well beyond apex of scutellum. Scutellum always moderately punctate *A. micropunctatus* sp.nov.
 - Central lobe of aedeagus hooked at tip (Fig. 14). First elytral stria virtually absent. Scutellum lacking punctures or weakly punctate with very small punctures *A. australicus* Blackburn.
- 3 — Central lobe of aedeagus hooked at tip (Fig. 9). Small punctures on sides of elytra relatively small, < 1/4 diameter of adjacent large punctures (Fig. 4). Serial punctures easily traceable at apex *A. austrinus* sp.nov.
 - Central lobe of aedeagus rounded, parameres straight. Small punctures on sides of elytra relatively large, many 1/2 size of adjacent punctures (Fig. 2). Serial punctures may be hard to trace at apex 4
- 4 — Basal portion of aedeagus shorter than parameres (Fig. 10). Size < 3.9 mm. Elytra often with a vague series of darker patches in alternate interstriae *A. duplopunctatus* Blackburn
 - Basal portion of aedeagus nearly twice length of parameres (Fig. 11). Size ≥ 3.5 mm. Elytra without series of dark patches. *A. queenslandicus* J. Balfour-Browne.

Amphiops austrinus sp. nov.

Description (number examined 5) Figs 4, 9

Length 3.4–4.0 mm. Broadly oval, elytra deep, almost as high as long. Reddish-brown, disk of pronotum a little darker as are serial punctures. Head broad, strongly punctate with variously sized punctures, confluent at front. Pronotum broad, punctures of various sizes, weak on disk

grading to strong laterally, systematic series distinct. Elytron very weakly punctured near suture, grading to strong laterally; in middle at side serial punctures strong, large, somewhat difficult to trace; large punctures separated by own diameter or a bit less, small punctures, which alternate with larger ones, are very much smaller; interstitial punctures of three distinct sizes, largest as large or larger than those in serial lines, separated by own width or less, small punctures more numerous, very much smaller, 1/4–1/3 diameter of large ones, in places third size group of minute (micro) punctures present.

Aedeagus squat, basal portion shorter than parameres. Apical portion of central lobe narrow, weakly tapering, considerably shorter than parameres, ending in small broad hook. Parameres broad in basal half, narrow in apical, strongly curved downwards near tip, tips truncated and a little enlarged.

Distribution

Only known for the type localities in south-east Queensland.

Types

Holotype: 'Brisbane 1/64, CW', SAMA.

Paratypes: 4, 'Qld Petrie, 10 km W, 23/11/95, C. Watts', SAMA.

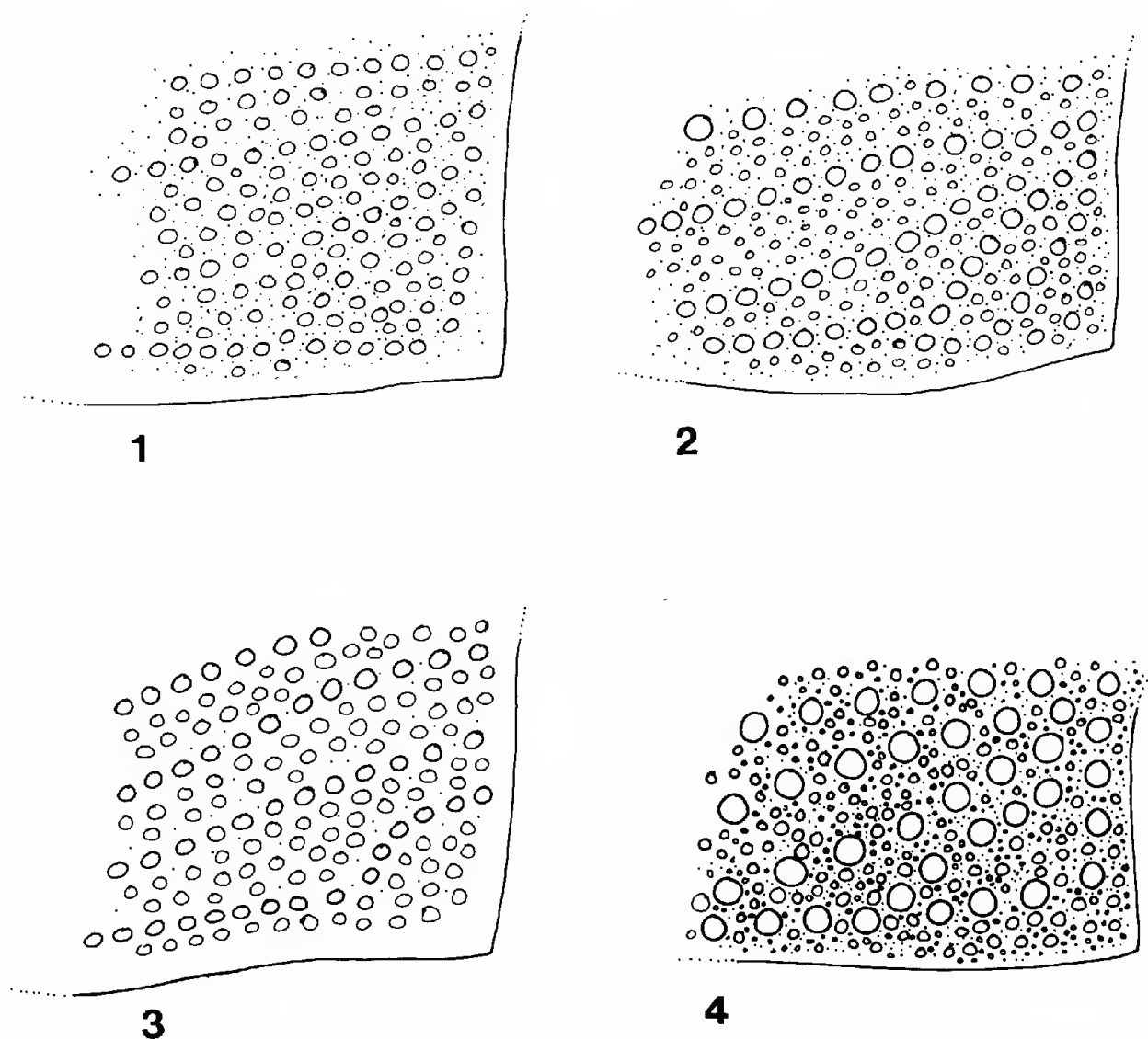
Remarks

In most characters similar to *A. duplopunctatus* and *A. queenslandicus*. Apart from the male genitalia *A. austrinus* differs from both of these by the greater contrast in size between the large and small interstitial punctures on elytra, caused primarily by the comparatively small size of the small punctures. In *A. duplopunctatus* and *A. queenslandicus* the small interstitial punctures become quite prominent towards the side and apex, often reaching half the size of the larger ones. In *A. austrinus*, apart from very near the elytron edge, the small punctures remain much smaller than the larger ones. The downward curve of the parameres and the apical hook on the tip of the central lobe of the aedeagus, also clearly set it apart from these two species.

Amphiops australicus Blackburn, 1898

Description (number examined 234) Figs 3, 14

Length 2.7–4.0 mm. Broadly oval, elytra deep, about as high as long. Brown, sometimes with distinct darker blotches on elytron, to black with



FIGURES 1-4. Pattern of punctures near anterior-lateral angle of elytron. 1, *Amphiops micropunctatus*; 2, *Amphiops duplopunctatus*; 3, *Amphiops australicus*; 4, *Amphiops austrinus*.

some vague lighter areas. Head broad, moderately to strongly punctate, punctures mainly small with scattered much larger ones, becoming stronger and denser in front, confluent and rugose along front margin. Pronotum broad, weakly punctured, punctures almost obsolete on disk but becoming stronger laterally, much smaller than eye facet, systematic punctures small, about size of eye facet. Elytra weakly punctured on disk, becoming stronger laterally. At side in middle, serial punctures about puncture-width apart, lacking alternating small punctures. Interstrial area usually only with large punctures which are approximately same size, and approximately same size as serial punctures, about a puncture-width

apart or somewhat greater. Areas of elytra near the scutellum and laterally may have indistinct micro punctures.

Aedeagus elongate, basal piece about same length as parameres. Central lobe narrow, narrowing to point, tip with upward hook, shorter than parameres. Parameres elongate, broad in basal half, narrow in apical, tips weakly expanded, curved downwards in apical fifth.

Type

Holotype female: '5074T', 'Adelaide R, NW Australia, J. J. Walker', 'Blackburn Coll 1910-236', '*Amphiops australicus*, Blackburn', with round type label, BM(NH). Seen.

*Distribution***Northern Territory**

11 km SW by S Borrooloola, ANIC; Cahills Crossing, ANIC; 7 km NW by N of Cahills Crossing, ANIC; Gimbar Stn, NTM; Howard Springs, SAMA; Holmes Jungle, NTM; Jabiru, NTM; Junction of Arnhem Hwy and Oenpelli Rd, NTM; Kakadu NP, NTM; Koongarra, ANIC; Magela Ck, ANIC; McArthur R, ANIC; 19 km E by S of Mt Borradaile, ANIC; 30 km WSW Mt Cahill, ANIC; 9 km N of E Mudginbarry HS, ANIC; Nourlangie Ck, ANIC; 18 km E by N Oenpelli, ANIC; Tindale, ANIC, NMV; UDP Falls, NTM; 12°40S 132°54E, ANIC; 12°06S 133°04E, ANIC.

Queensland

12°08S 142°16E, ANIC; 12°22S 142°37E; 12°06S 142°33E, ANIC; 14°51S 142°58E, ANIC; 18°33S 138°11E, ANIC; Archer Bend, SAMA; Batavia Downs HS, ANIC; Barron Falls, ANIC; Bertiehaugh Ck, ANIC; Cairns, ANIC; 110 km S Coen, NMV; East Claudie R, UQIC; 110 km S Coen, NMV; 70 km SW Greenvale, SAMA; Hann R, ANIC; Lakfield NP, QDPIM; 50 M N. Laura, UQIC; 72 km NW Laura, ANIC; 21 km E Mareeba, QDPIM; Moreton, ANIC; 2 km NNE Mt Tozer, ANIC; 9 km ENE Mt Tozer, ANIC; 3 km NE Mt Webb, ANIC; 10 km WNW Rokeby, ANIC; Wenlock R, ANIC.

Western Australia

14°25S 126°40E, ANIC; 14°52S 125°50E, ANIC; 14°52S 125°50E, ANIC.

Remarks

Among Australian *Amphiops*, *A. australicus* can only be confused with *A. micropunctatus* due to the virtual lack of small and micro punctures on the elytra. *Amphiops micropunctatus* has more extensive micro punctures over the elytra but these can be missed if the specimen is at all dirty or the light poor. The two species are best separated by the much more strongly punctate scutellum and the quite well developed first elytral stria on *A. micropunctatus*, compared to the virtually impunctate scutellum region in *A. australicus*. I have not seen any black specimens of *A. micropunctatus* but light coloured *A. australicus* are occasionally encountered, usually with well marked dark patches on elytra. The tip of the aedeagus in *A. australicus* is hooked, in *A. micropunctatus* it is not.

***Amphiops duplopunctatus* Blackburn, 1898**

Description (number examined 65) Figs 2,10

Length 3.0–3.9 mm. Broadly oval, clytra deep, as high as long. Dark reddish-brown, elytra with vague lighter patches. Head broad, strongly punctate, punctures of varying size, often becoming confluent along front margins. Pronotum broad, weakly punctured on disc, becoming stronger laterally, punctures of various sizes, systematic series moderately distinct, relatively small, about same size or a little larger than eye facets. Elytra weakly and shallowly punctured on disc, becoming much stronger towards sides. At side, in middle, serial punctures large, easy to trace, each separated by own width or less, alternating with a small puncture. Interstitial punctures of three sizes, largest a bit smaller than serial punctures and most separated by more than their width, small punctures much more numerous and 1/3–1/2 diameter of large ones, numerous and relatively large micro punctures.

Aedeagus with basal piece shorter than parameres, apical portion of central lobe narrowing to thin point, lacking any apical thickening or hook, shorter than parameres. Parameres wide in basal half, narrow in apical half, tips rounded not curved.

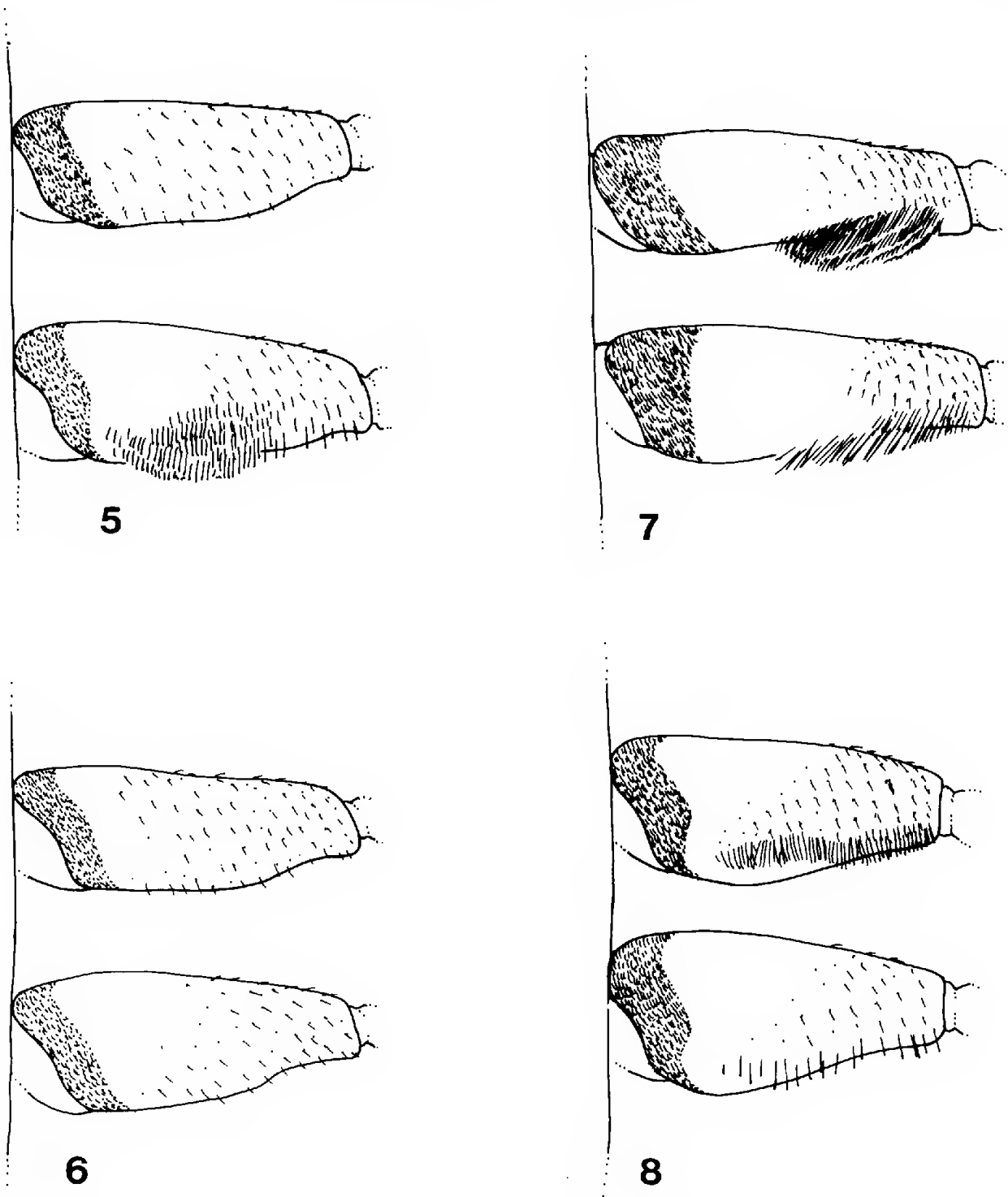
Types

Holotype female: '6370 Qu. T.', 'Blackburn Coll 1910–236', 'Amphiops duplopunctatus, Blackburn', BM(NH). Seen.

Lectotype: 'Queensland Blackburn's Coll.', 'Amphiops duplopunctatus BL. co-type', dissected and remounted, SAMA. Seen.

*Distribution***Northern Territory**

Daly R Crossing, NTM, ANIC; Darwin, ANIC, NTM, SAMA; 11 km NE of E of Darwin, ANIC; Gimbat Stn, NTM; Holmes Jungle, ANIC, NTM, SAMA; Howard River, NTM; Howard Springs, NTM, SAMA; Humpty Doo, NTM, QDPIM; 10 km N of Jabiru, NTM, QDPIM; 29 km W by N Jabiru, NTM, ANIC; Keep River NP, NTM, ANIC; Magela Ck, ANIC; 12 km NNW Mt Cahill, NTM, ANIC; 19 km WSW Mt Cahill, ANIC; 9 km N by E of Mudginbarry, ANIC; Nabarlek Dam, ANIC; 6 km SW by S Oenpelli, ANIC; Sth Alligator R, ANIC; 15 km SE Wangi, NTM; Yungaburra, NTM, QDPIM; 16°02S 130°23E, NTM.



FIGURES 5–8. Ventral view of mesofemur (top) and metafemur (bottom). 5, Male *Allocotocerus yalumbaboothbyi*; 6, Female *Allocotocerus yalumbaboothbyi*; 7, Male *Allocotocerus tibialis*; 8, Female *Allocotocerus tibialis*.

Queensland

Bamaga, SAMA, UQIC; Barringtonia Lagoon W Cape York, QM; Batavia Downs HS, ANIC; Bertihaugh Ck, ANIC; 8 km N Bluewater, SAMA; 9km N Bluewater, SAMA; Burster Ck,

ANIC; Caloundra, SAMA; Claudie R, UQIC; Dalhousie R, ANIC; East Claudie R, UQIC; Flinders Is, SAMA; 12 km SW Heathlands, ANIC; Holroyd R, ANIC; Iron Range, UQIC; Jordine R, UQIC; Kuranda, SAMA; Lawn Hill,

ANIC; Lake Barrine, ANIC; Lake Tinaroo, ANIC; 73km NW of W Laura, ANIC; Lockerbie, UQIC; 9 km NNW Lockhart R, ANIC; 18 km N Mareeba, QDPIM; Mazlin Ck, QDPIM, ANIC; 3 km ENE Mt Tozer, ANIC; 9 km ENE Mt Tozer, ANIC; 11 km ENE Mt Tozer, ANIC; Murphy's Ck, UQIC; Normanby R, ANIC; Pascoe R, ANIC; N Pine River, QM; Redcliffe, UQIC; Ripley, SAMA; 27km NW by W Rokeby, ANIC; Schramm Ck, ANIC; Townsville, SAMA, 20km S Townsville, SAMA; 3 km WSW Ussher Point, ANIC; Wenlock R crossing, ANIC; 18°35S 138°03E, ANIC; 18°40S 138°20E, ANIC.

Western Australia

Carson Escarpment, ANIC; Drysdale R, ANIC;

Remarks

If reference material is available *A. duplopunctatus* can be relatively easily separated from *A. austrinus* by its stronger interstitial punctation, but lacking reference specimens it can only be separated with certainty from this species by its aedeagus.

Typical *A. duplopunctatus* are smaller, higher and often darker than *A. queenslandicus* and have stronger large punctures on elytra. In many *A. duplopunctatus*, particularly from the Northern Territory, many of the large serial punctures on the sides of the elytra are less than a puncture-width apart, a condition I have not seen in any *A. queenslandicus*. Except for particularly dark specimens, *A. duplopunctatus* usually has quite regular darker blotches in alternate elytral interstriae variably distinct. *Amphiops queenslandicus* lacks these and has more uniformly coloured elytra although the punctures are often darker particularly laterally. *Amphiops duplopunctatus* is also smaller than *A. queenslandicus* (<3.9 mm as compared to >3.5 mm).

Balfour-Browne (1939), considered *A. duplopunctatus* to be possibly no more than a subspecies of *A. australicus*, an opinion based mainly on a perceived close similarity of the male genitalia. The male genitalia of what I take to be *A. australicus* and *A. duplopunctatus* are clearly distinct (the types are female). The markedly different punctation also differentiates the two species.

Amphiops micropunctatus n. sp.

Description (number examined 30) Figs 1, 13

Length 2.7–4.3 mm. Oval, elytron deep, a little

longer than high. Reddish-brown, punctures on elytron darker. Head broad, moderately strongly punctate, punctures tending to be either big or small, smaller predominating, becoming confluent on front margin. Pronotum broad, moderately punctate, punctures of varying sizes, stronger laterally, systematic series distinct, comparatively large, many over twice size of adjacent punctures, nearly twice size of eye facet. Elytra weakly and shallowly punctured on disc, becoming much stronger towards sides. Laterally in middle serial punctures large, easy to trace, about a puncture-width apart; interstitial area shiny, punctures of two sizes, the larger sparse, most > 2x width apart, somewhat smaller than striae, the smaller, more numerous, very small (micro), in contrast to other punctures, becoming obsolete laterally.

Aedeagus with basal piece about same length as parameres, parameres wide in basal half, narrow in apical, tips broadly rounded, central lobe narrow, tip bluntly pointed, reaching nearly to end of parameres.

Remarks

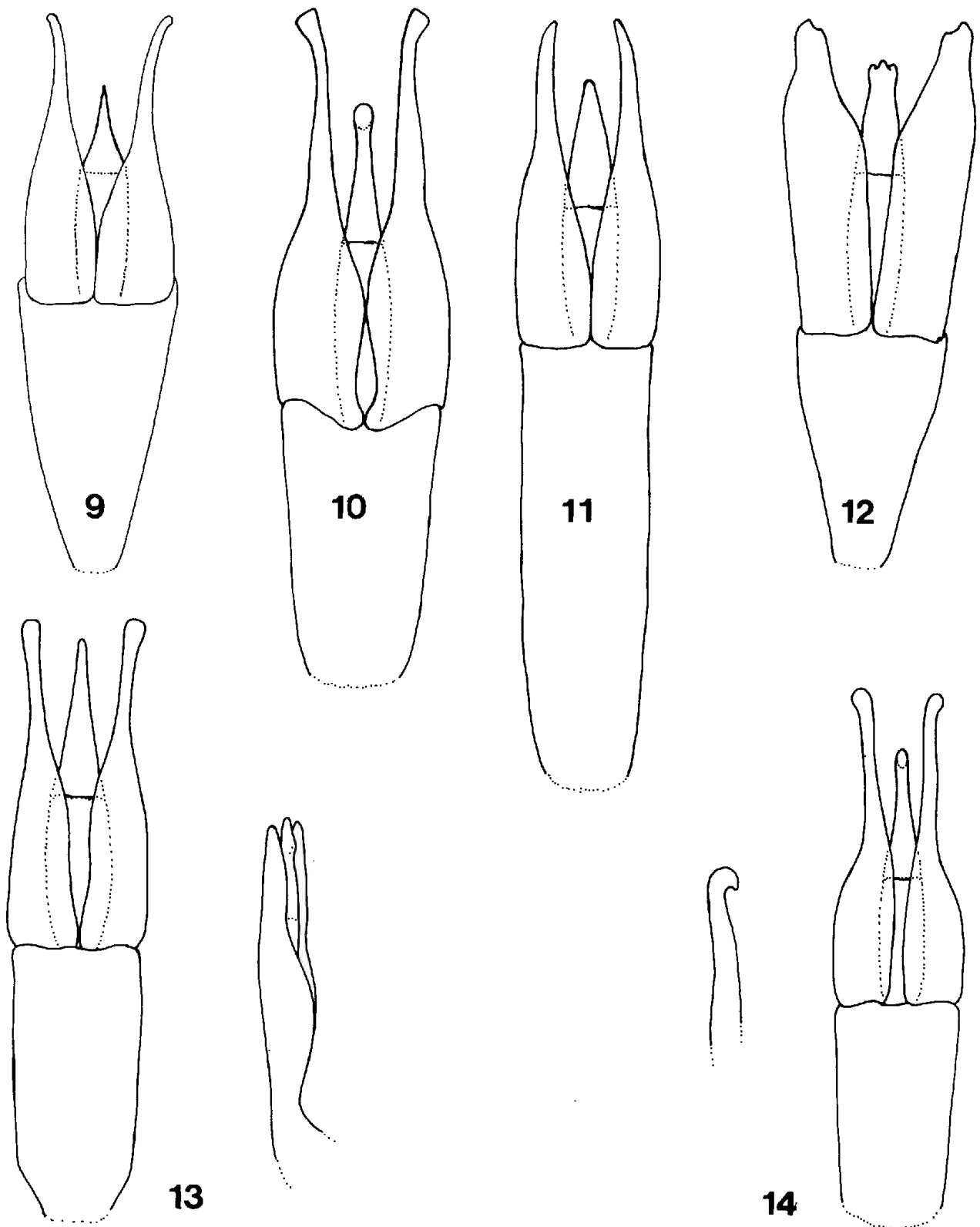
In colour and size resembling *A. duplopunctatus* but differing from it in punctation and in the shape of the aedeagus which has the central lobe larger than in *A. duplopunctatus*. The absence of the 'small' size of interstitial punctures in the species resembles *A. australicus* and readily separates these two species from the other Australian *Amphiops* which have the interstitial areas much more punctate. From *A. australicus* (and most other Australian *Amphiops*) it differs by having the first (sutural) elytral stria quite well developed as well as a greater development of very small (micro) punctures on the elytra, although an occasional *A. australicus* may have quite extensive micro punctation.

This species is only known from a limited area of North Queensland. Judging from the localities it is possible that it is a closed forest species. The specimens from the West Claudie basin and Lockhart River were taken in October from still pools in closed forest. No other habitat information is available.

Types

Holotype male: 'Australia, N Qld 15 km WNW of South Johnstone "Light Trap"', 'Fay and Halfpapp 1986', QDPIM.

Paratypes: 2 same data as holotype, QDPIM; 1, 'Australia N Qld Tolga 3', '1986 J. D. Brown light Trap', QDPIM; 1, 'Cow Bay, N of Daintree



FIGURES 9-14. Ventral view of aedeagus. 9, *Amphiops austrinus*; 10, *A. duplopunctatus*; 11, *A. queenslandicus*; 12, *Regimbartia attenuata*; 13, *Amphiops micropunctatus*; 14, *A. australicus*.

N Qld, 15–22nd March 1984 I. C. Cunningham', QDPIM; 2, '12°43'S 143°17'E, 9 km ENE of Mt Tozer 5–10th July 1986 T Weir and A. Calder', ANIC; 3, '12.44S 143.14E 3 km ENE of Mt Tozer 28th Jun – 4th July 1986 T Weir and A. Calder', ANIC; 10, '15°03'S 145°09'E 3 km NE Mt Webb 30th April – 3rd May 1981 A Calder', 8 ANIC, 2 SAMA.

Distribution

Queensland

Dead Horse Ck, ANIC; East Claudie R, UQIC; Gordon Ck nr Claudie R, UQIC; Iron Range, UQIC; 9km NNW Lockhart R, ANIC; 3.5km SW by S Mt Baird, ANIC; 2km NNE of Mt Tozer, ANIC; 6km ENE Mt Tozer, ANIC; 11km ENE Mt Tozer, ANIC; Mt Webb Nat. Pk, ANIC; West Claudie R, ANIC.

Amphiops queenslandicus Balfour-Browne, 1939

Description (number examined 34) Fig. 11

Length 3.5–5.3 mm. Broadly oval, elytra deep, almost as high as long. Dark reddish-brown, elytra with vague darker/lighter areas and many serial punctures black. Head broad, strongly punctate, punctures of varying sizes becoming confluent along front margin. Pronotum broad, moderately punctate on disc becoming stronger toward sides, systematic punctures moderate, about 3x size of adjacent punctures, a little larger than eye facet. Elytra with small but sharp punctures on disc becoming much stronger laterally. At sides in middle, large serial punctures relatively small, most separated by more than their widths, small alternating punctures relatively large, some approaching 1/2 width of larger ones; interstitial punctures of three sizes: large, larger than serial punctures, separated by more than their width, small much more numerous, relatively large, 1/4–1/2 diameter of large ones, micro punctures present over most of elytra.

Aedeagus elongate, basal piece nearly twice length of parameres. Central lobe shorter than parameres, narrowing to a point, apex not swollen or hooked. Parameres broad basally, becoming narrower apically, tips rounded, weakly curved downwards.

Types

Holotype male: 'Queensland Australia', 'Amphiops queenslandicus Type J. Balfour-Browne det.', with round Type label and a

handwritten locality (which I cannot read), BM(NH). Seen.

Paratypes: 6, same data as Holotype (except handwritten label and Type designation); 1, male, 'Rockingham austral', 'Australia' *Amphiops queenslandicus* M. J. Balfour-Browne det., all in BM(NH) with round paratype labels. Seen.

Distribution

Northern Territory

S Alligator R, QM; Black Point Coburg Pen, ANIC; 5km NNW Cahills Crossing, ANIC; 7km NW by N Cahills Crossing, ANIC; Coastal Plains Research Station, ANIC; Daly R Mission, ANIC; Darwin, SAMA; Fogg Dam, NTM; Howard Springs, SAMA; Humpty Doo, ANIC; Jabiru, NTM; Jim Jim, ANIC, NTM; Kakadu NP, NTM; Kapalga, QM; Koongarra, ANIC; 12km NNW Mt Cahill, ANIC; 19km WSW Mt Cahill, ANIC; 9km N by E of Mudginbarry HS, ANIC; Oenpelli, AM; 6km SW by S Oenpelli, ANIC; 12°40'S 132°22'E, QM.

Queensland

Ashgrove, QM; Ayr UQIC; Bowen, SAMA; Brisbane, UQIC; Bulburin St Forest via Many Peaks, UQIC; Caloundra, SAMA; Cooloola, QM; East Claudie R, UQIC; Gatton, UQIC; Homehill, SAMA; Ingham, UQIC; Ipswich, AM; Iron Range, UQIC; Lockerbie UQIC; Many Peaks, UQIC; S Pine R, QM; Ripley, SAMA; Rockhampton, ANIC, SAMA; 20 km S Townsville, SAMA; 37 km S Townsville, SAMA.

Remarks

The distinctive male genitalia readily identify this species. *Amphiops duplopunctatus* is smaller with the elytra not quite as deep, elytral punctures weaker and usually differently coloured (see under *A. duplopunctatus*).

Amphiops queenslandicus also closely resembles *A. austrinus* but in this case the weaker, smaller punctures on the elytra of *A. austrinus* seem different enough to enable reliable separation. However, the male genitalia should be used wherever possible.

Regimbartia Zaitzev, 1908

Regimbartia attenuata (Fabricius, 1801)

= *Volvulus scaphiformis* Fairmaire, 1879. Synonymy after d'Orchymont, 1932.

Description (number examined 89) Fig. 12

Length 3.6–5.0 mm. Narrowly boat-shaped, high, sides of elytra subparallel, perpendicular, black, shiny, appendages testaceous. Head deflexed, eyes large, punctures moderate scattered, weaker on disc, those forward of eye about size of eye facet, systematic punctures inward from eye relatively small, about size of eye facet. Pronotum broad, weakly and sparsely punctured on disc, more strongly towards sides where they are about same size as on front of head; systematic punctures few and hard to trace. Elytra more strongly punctured, somewhat stronger at sides than on disc, each elytron with 10 serial lines, inner two incomplete anteriorly, for the most part serial punctures joined forming sharp grooves. Mesosternum with strong narrow keel, apical sternite with short sharp spine in midline at apex.

Male: Protarsi with two basal segments moderately expanded dorso-ventrally.

Types

Hydrophilus attenuata Fabricius. Ceylon. Type not located.

Volvulus scaphiformis? Holotype. Rockhampton Fairmaire, ?in Museum Godeffroy. Not seen.

*Distribution***Northern Territory**

Bessie Springs, ANIC; 11 km SW by S of Borroloola, ANIC; 30 km NE by E of Borroloola, ANIC; 48 km SW by S Borroloola, ANIC; 1 km N of Cahills Crossing, ANIC; 7 km NW by N Cahills Crossing, ANIC; Daly River, NTM; Darwin, ANIC, SAMA; Elsey Creek, ANIC; Fergusson R, ANIC; Fogg Dam, ANIC, NTM; Howard Springs, SAMA; Jabiru, NTM; Katherine, NTM; Keep River NP, ANIC; Lake Bennett, NTM; Magela Ck, ANIC; Manton Reservoir, NTM; 2 km N Mudginberri HS, ANIC; 6 km N by E Mudginberri, ANIC; Nourlangie Ck, ANIC; Roper R, ANIC; South Alligator R, QM; U.D.P. Falls, NTM;

Queensland

Archer Bend, SAMA; Ayr, UQIC; Brisbane, MV, QM, UQIC; Cairns, ANIC, QM; Calliope R, ANIC; Caloundra, SAMA; Cape Flattery, DPIM; Chillagoe, DPIM; Claudie R, UQIC; East Claudie R, QIC; Clermont, AM; Cooktown, MV; 40M N Cooktown, UQIC; Duaringa, AM; Edungalba, ANIC; Einasleigh, DPIM; Frenchman's Creek via Rockhampton, UQIC; Gin Gin, UQIC; Gregory River Hotel, DPIM; Homehill, SAMA; Kirrama

Rng, QM; Karumba, UQIC; Lakefield NP, ANIC; Mackay, SAMA; Marceba, ANIC, DPIM; 18km N Mareeba, DPIM; Mary Ck, ANIC; Melvor R, UQIC; Mt Garnet, SAMA; 3.2 km SW of Mt Inkerman, ANIC; Mt Molloy, ANIC, QM; 3 km ENE Mt Tozer, ANIC; 6 km ENE Mt Tozer, ANIC; Nordello Lagoon, DPIM; 11km WSW Petford, DPIM; N Pine R, QM, UQIC; Rockhampton, SAMA; 67 km E Roma, QM; Samford, UQIC; Silver Plains CP, DPIM; 15km WNW South Johnstone, DPIM; Starbright HS, DPIM; Strathmore Stn, DPIM; Tolga, DPIM; Townsville, QM; Walkamin, DPIM; 40km S Weipa, DPIM; Yaamba, UQIC; Yeppoon, UQIC; 18°38 S 138°11 E, ANIC; 18°34 S 138°08 E, ANIC.

Western Australia

Channley R, ANIC; Derby, SAMA; Fitzroy R, ANIC; 12 km S Kalumburu Mission, ANIC; Kunanurra, DPIM; 1 km NNE Millstream, ANIC; Synnot Ck, ANIC; 14°53 S 125°45 E, SAMA.

New South Wales

Eccleston, UQIC.

Remarks

Once known, this distinctive water beetle is unlikely to be confused with any other Australian species. It is relatively common in shallow swamps and dams along the coast from northern New South Wales to the Kimberley. Beyond Australia the species has a wide distribution in South-east Asia as far west as Sri Lanka.

I have followed d'Orchymont (1932 p. 709) for the name of this widespread species.

***Allocotocerus* Kraatz, 1883**

The three Australian species of *Allocotocerus* (= *Globaria* Latreille) are all moderately sized, highly spherical insects with the ventral surface shiny black. Within Australia they can only be confused with species of *Amphiops*, particularly *A. queenslandicus* which is of a similar size and shape. The even, regular punctation, uniformly black ventral surface, and swimming hairs on the legs in *Allocotocerus* readily separate them from *Amphiops*.

There is little to separate the species other than the sexual characters of the aedeagus, trochanter setae and the labrum.

The first described and best known species, *A. punctatus*, is common and widespread in slowly

moving water and in swamps in eastern Australia from northern New South Wales northwards. It appears to be absent from the Northern Territory and northern Western Australia where its place is taken by *A. tibialis* and *A. yalumbaboothbyi*. Conversely these species likewise have not been recorded from the east coast.

An additional species (the type species, *A. bedeli* Kraatz 1883) occurs in New Guinea. Unfortunately the holotype does not appear to be in the Deutsches Entomologisches Institut in Eberswalde. In its place is a label written by Korschefsky in 1937 indicating it was lost (Lothar Zerche pers. com.). The recognition of this species and any possible influence on the nomenclature of Australian species must await the collection of further specimens from New Guinea.

KEY TO AUSTRALIAN ALLOCOTOCERUS

- 1 — Labrum strongly extended forward, strongly bifid male *A. punctatus* (Blackburn)
- Labrum normal, often hidden beneath clypeus, not bifid 2
- 2 — Protibia light yellow with darker apical portion *A. punctatus* (Blackburn)
- Protibia lighter than other legs but without darker apical portion 3
- 3 — Setae on outer posterior angle of ventral surface of mesofemur more developed than those on metafemur (Figs 7 & 8). Aedeagus with parameres broad with rounded tips, central lobe sharply pointed, much shorter than parameres (Fig. 16) *A. tibialis* (Balfour-Browne)
- Setae on metafemur equally poorly or slightly more developed than on mesofemur (Figs 5 & 6). Aedeagus with parameres narrowing to point, central lobe broad with narrow spine at tip, as long as parameres (Fig. 17) *A. yalumbaboothbyi* sp. nov.

Allocotocerus punctatus (Blackburn, 1888)

Description (number examined 112) Fig. 15

Length 3.5–4.5 mm. Oval, elytra high, height only a little less than length. Black, shiny, appendages lighter, yellowish with darker terminal portion to tibia. Head narrow, front margin broadly and quite deeply concave, sides of clypeus narrowly margined, rather evenly covered with moderate punctures which are weaker in middle than at sides, those forward from eyes a

bit larger than size of eye facet, systematic punctures virtually absent. Pronotum narrower than elytra, punctures on disc much weaker than on head, becoming considerably stronger towards front corners, systematic punctures few, sparse and hard to find. Elytra covered with very even punctures in same area but much stronger laterally than on disc, serial punctures 1.5–2x diameter of adjacent punctures, reduced to 2–3 short lines midway along side of elytron. Midline of mesosternum with strong, tall spike between mesocoxae. First ventrite constricted in middle with rather wide strong midline carina. Metasternum with two strong carinae in midline with deep gap between them, the anterior one cylindrical and angled backwards, the posterior one anvil shaped in lateral view.

Male: Labrum prominent, front edge deeply bifid. Protibia triangular in cross-section. Aedeagus with basal portion strongly bent, 2.5x length of parameres which are broad for whole length, central lobe broad except for short very narrow portion at apex. Meso- and meta-trochanters with widely scattered short, stout setae on ventral face.

Female: Labrum little exposed, front edge not bifid. Protibia of normal shape, contrast between dark apical portion and yellow on rest of proleg often less pronounced than in male. Meso- and meta-trochanters with scattered, sparse, short, stout setae on ventral face.

Type

Holotype: 'T2328', 'Blackburn coll 1910–236', 'Volutus punctatus, Blackburn', BM(NH). Seen.

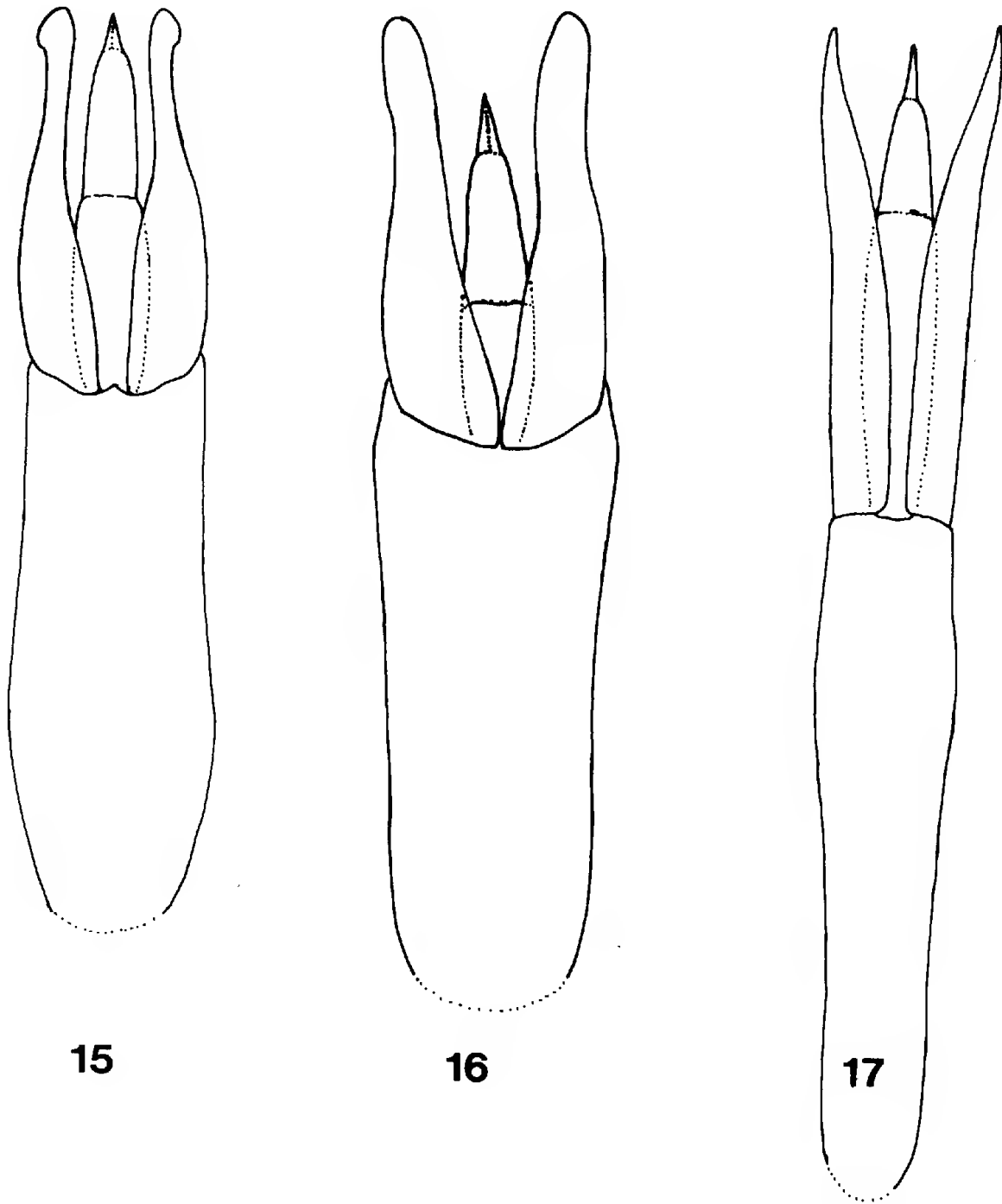
Distribution

Queensland

8 km N Bluewater, SAMA; Cardstone, ANIC; 40 km N Coen, SAMA; 70 km N Coen, SAMA; Caloundra, SAMA; 29 km NW by W Cooktown, ANIC; 40 km N Cooktown, SAMA; Ingham, ANIC; Lakefield NP, QDPIM; 18 km N Mareeba, QDPIM, ANIC; Mary Ck, ANIC; Mc Ivor R, ANIC; Townsville, MV; Moorehead R, ANIC; Moreton, ANIC; Mt Coolum, ANIC; 20 km S Townsville, SAMA; 37 km S Townsville, SAMA; Wenlock R Crossing, ANIC; 15°17S 145°10E, ANIC.

Remarks

In overall shape, punctuation and colour closely similar to *A. tibialis* and *A. yalumbaboothbyi* but the male characters readily separate it from these species. Male *A. yalumbaboothbyi* and *A. tibialis*



FIGURES 15–17. Ventral view of aedeagus. 15, *Allocotocerus punctatus*; 16, *Allocotocerus tibialis*; 17, *Allocotocerus yalumbaboothbyi*.

lack the very distinctive labrum and protibia of male *A. punctatus*. In *A. punctatus* the dark apical portion of the protibia separates both male and female from the other species which have more uniformly coloured protibiae. In both male and female *A. tibialis*, the number and density of setae on the trochanters are much larger than in *A. punctatus*.

The species is relatively common in coastal

dams and swamps from northern Southern Queensland to Cape York, often found together with the similarly shaped *Amphiops*.

Allocotocerus tibialis (Balfour-Browne, 1939)

Description (number examined 61) Figs 7, 8, 16

Length 4.5–5.0 mm. Oval, clytra high, height

only a little less than length. Black, shiny, appendages dark-testaceous. Head narrow, front edge widely and moderately concave, sides of clypeus margined, strongly punctured, punctures in front of eyes larger than eye facet, systematic punctures inwards from eye few and hard to trace, punctures on disc somewhat weaker than elsewhere, about size of eye facet. Pronotum narrow, somewhat more weakly punctured than head particularly on disc, systematic punctures few and hard to find. Elytron punctured rather more strongly than on pronotum and head, punctures much weaker on disc than on sides where they are strong and less than a puncture-width apart. Serial punctures few or absent, if present little larger than adjacent punctures. Mesosternum with moderately tall, sharp spine in midline. Midline of metasternum with two distinct carinae, separated by deep gap, anterior carina cylindrical and angled strongly backwards, posterior one broader and curving backwards and upwards when viewed from side. First abdominal ventrite narrowed in middle half, midline with rather narrow and strong carina, ventrites two and three narrowed in central half, weakly bulbous/carinate in midline. Area between ventrites deeply grooved. Fourth ventrite weakly narrowed anteriorly, smooth.

Male: Labrum simple. Protibia a little flattened and widened, tarsi unmodified. Mesotrochanters stout with a well-marked group of long golden setae on anterior apical ventral angle, inner half of ventral face lacking punctures/setae. Metatrochanters stout with a less well-developed group of setae in same place, metatibia stout. Aedeagus long, sinuate, relatively broad, basal piece about 1.5x length of parameres, parameres broad, subparallel, rounded at tips, central lobe narrowing progressively to tip, shorter than parameres.

Types

Holotype male: 'Adelaide River 92-2', '4969', 'Globaria tibiale mihi J. Balfour-Browne det.' with red type label, BM(NH). Seen.

Lectotypes: 1, 'Adelaide River, NW Australia J. J. Walker', 'G. C. Champion Coll. B.M. 1927-409' with red (allotype) type label, BM(NH), 10 same data, in BM(NH); 3, same data as holotype, BM(NH). Seen.

Distribution

Northern Territory

Gimbat Stn, NTM; 6 km E Humpty Doo,

QDPIM; Jabiru, NTM; 10 km N Jabiru, QDPIM; Junction of Arnhem Hwy and Oenpelli Rd, NTM; Magela Ck, ANIC; 19 km E by S Mt Borradaile, ANIC; 8 km E Mt Cahill, ANIC; 46 km WSW Mt Cahill, SAMA; Nabarlek Dam, ANIC; Nourlangie, ANIC; UDP Falls, NTM; Wildman R, NTM.

Remarks

Both male and female *A. tibialis* can be separated from *A. punctatus* and *A. yalumbaboothbyi* by the more extensive development of setae on the mesotrochanters. The elytral striae are also usually much weaker or absent in this species but at least traceable in the others. The species has not been recorded from the east coast and appears to have a rather restricted distribution in coastal Northern Territory. Here it occurs commonly, often with *A. yalumbaboothbyi*.

Amphiops tibialis can also be separated from the very similar *A. yalumbaboothbyi* by the differently shaped posterior mesosternal protuberance: in *A. tibialis* this is thicker and curved upwards behind in lateral view whereas it is straight in *A. yalumbaboothbyi*.

Allocotocerus yalumbaboothbyi sp. nov.

Description (number examined 51) Figs 5, 6, 17

Length 3.5–4.5 mm. Oval, elytra high, only a little longer than high. Black, shiny, ventral surface and appendages dark-testaceous, proleg yellowish. Head narrow, front margin broadly and quite deeply concave, rather evenly covered with moderate punctures which are a little weaker on disc than at sides, those forward from eyes a bit larger than size of eye facet, systematic punctures virtually absent. Pronotum narrower than elytra, punctures on disc much weaker than on head, becoming considerably stronger towards front corners, systematic punctures few and hard to find. Elytra covered with very even punctures which become much stronger laterally, serial punctures reduced to 2–3 short lines on each elytron towards sides in middle; midline of mesosternum with tall sharp spike forward of mesotrochanters, midline of metasternum with two strongly raised carinae separated by short deep gap, front carina in shape of backwardly inclined broad spine, rear carina oval shaped on a broad pedestal when viewed laterally. First ventrite moderately constricted in middle with a narrow but well marked central carina extending

forward between metatrochanters. Second sternite also constricted but without carina, fourth not restricted. Sutures between ventrites wide, deep, well-marked.

Male: Labrum small, usually contracted, not bifid, protibia not expanded, basal two segments of protarsi a little expanded with ventral hairs. Mesotrochanters with a few scattered, short spines on apical ventral surface. Mesotrochanters with longer more numerous setae forming a sparse brush along posterior ventral portion of metatrochanter. Aedeagus long, sinuate with relatively broad basal portion which is about 2.5x length of parameres. Parameres narrow, evenly narrowing to quite sharp tip. Central lobe as long as parameres. In a number of specimens the parameres are twisted and splayed out, presumably an artefact of preservation, but one that I have not seen in other species.

Female: Basal segment of protarsi not weakly expanded, with ventral hairs. Mesotrochanters with a few sparse, stout setae on ventral face at apex, metatrochanter with similar setae restricted to apical half.

Types

Holotype male: '12°22S 133°01E 6 km SW by S of Oenpelli NT, 30.v.73, at light E. G. Matthews', SAMA.

Paratypes: 4, 'W Australia Mitchell Plateau 14°40S 125°44E 23 Sept 1982 B. V. Timms', SAMA; 4, '13°34S 132°15E', 'Moline Rockhole' 6 km E by E of Mt Daniela 23.v.1974, NT T. Weir and T. Angeles', NTM; 6, '12°32S 132°50E Koongarra 15 km E of Mt Cahill NT, 15.xi.1972, T. Weir and A. Allwood', NTM; 11, 'NT UDP Falls, 18–19th July 1980, M. B. Malipatil Freshwater Pool', NTM; 20, '12°49S 132°51E, 15 km E by N of Mt Cahill NT, 29.x.72, light trap, E. Britton', ANIC.

Distribution

Northern Territory

8 km E by N of Mt Cahill, NTM; 19 km E by N Mt Cahill, NTM; Junction of Amhem Hwy and Oenpelli Rd, NTM; Kambolgie Ck, SAMA; Koongarra, NTM; Wildman R, NTM.

Remarks

Virtually indistinguishable from *A. tibialis* and *A. punctatus* other than by sexual characters. Males can be easily separated from *A. punctatus* by the lack of a large bifid labrum, from *A. tibialis* by the weaker development of setae on the mesotrochanters. In *A. tibialis* the mesotrochanter setae are longer and denser often to the extent of matting together. They are also more restricted to the apical portion of both meso- and metatrochanters than in *A. yalumbaboothbyi*.

Separation of female specimens is more difficult. Female *A. punctatus* have the prolegs pale yellow with a more or less obviously darker terminal portion to the tibia. In both *A. yalumbaboothbyi* and *A. tibialis* the tibiae lack the darker apical portion. The setae on both meso- and meta-trochanters of female *A. yalumbaboothbyi* and *A. punctatus* are small and sparse. In *A. tibialis* they are more developed particularly on the mesotrochanter.

ACKNOWLEDGMENTS

The curators of the collections listed earlier provided ready access to specimens in their care. Ms D. Churches and Ms C. Horne typed the manuscript and Mr R. Gutteridge prepared the drawings. Mrs M. Anthony and Mrs J. Evans helped with library aspects. Dr E. Matthews greatly improved the manuscript. I thank all these people without whom my task would have been much greater.

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DOUGLAS MAWSON: THE GEOLOGIST AS EXPLORER

D. W. CORBETT

Summary

Douglas Mawson was a born explorer. His professional career as a geologist and academic in Australia demonstrates this aspect of his character as clearly as his exploits in the Antarctic. Science and exploration dominated his life and motivated his endeavours, and the inseparable link between them was his pursuit of knowledge of glaciation-both ancient and modern. This paper reviews the diversity and wide geographical extent of his geological investigations, principally in South Australia, during the first half of the twentieth century at a time when the geology of large areas of the State was still largely unknown. The manner of his achievement and his distinguished contribution to the advance of geological knowledge in South Australia exemplify Mawson as the explorer-geologist.

DOUGLAS MAWSON: THE GEOLOGIST AS EXPLORER

D. W. CORBETT

CORBETT, D. W. 1998. Douglas Mawson: the geologist as explorer. *Records of the South Australian Museum* 30(2): 107–136.

Douglas Mawson was a born explorer. His professional career as a geologist and academic in Australia demonstrates this aspect of his character as clearly as his exploits in the Antarctic. Science and exploration dominated his life and motivated his endeavours, and the inseparable link between them was his pursuit of knowledge of glaciation—both ancient and modern. This paper reviews the diversity and wide geographical extent of his geological investigations, principally in South Australia, during the first half of the twentieth century at a time when the geology of large areas of the State was still largely unknown. The manner of his achievement and his distinguished contribution to the advance of geological knowledge in South Australia exemplify Mawson as the explorer-geologist.

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Douglas Mawson was a geologist with a broad scientific background and diverse interests within his discipline, as a review of his publications will verify (see Innes and Duff 1990). Known and honoured as one of the great Antarctic explorers, the prime motivation behind his achievement was the pursuit of scientific knowledge, which he coupled with the innovative use of the latest available technology. With the exception of Otto Nordenskjöld, geologist and leader of the Swedish Antarctic Expedition (1901–03), Mawson was the only science-trained expedition leader in the heroic age of South Polar exploration and his approach marked the beginning of the modern age of Antarctic exploration.

Mawson's career as a geologist and his scientific reputation were built in South Australia during his many years in the geology department at the University of Adelaide. While this paper focusses on the academic aspects of Mawson's life more than his Antarctic exploits, it is impossible to disentangle the two strands of endeavour. Down south he was the scientific-explorer; in the arid outback of South Australia he was the explorer-scientist. His major researches inextricably linked the two vastly different environments, for it was the opportunity to study an ice-age at first-hand and to equip himself better as an interpreter of past glaciations that inspired Mawson to venture south with Shackleton in 1907.

The circumstances of time and place (early twentieth century South Australia, much of it little

known geologically) and his life-long interests in glaciation, ancient and modern, determined that Mawson the geologist and Mawson the explorer were one and the same and through his extensive investigations in South Australia he personifies both the adventurous and the enquiring spirit.

Mawson's Antarctic exploits have been chronicled by historians, fellow-expedition members and in his own classic account 'The Home of the Blizzard'. His career as a scientist, and notably an assessment of his geological work, have been less well treated, although aspects of them are covered in the biography by his wife (Mawson 1962) and by Alderman (1967); by Parer and Parer-Cook (1983); in the biographical summary by Jacka (1986) and by Sprigg (1986). This paper presents a review, with emphasis on Mawson's career as a geologist in South Australia and his contribution to geological knowledge of the State.

Early Years

As one of the first generation of geologists trained in Australia, Mawson brought an Australian rather than European perspective to his work. Although born in Yorkshire, England on the 5th May, 1882, he was only two years old when his family migrated to Sydney and he grew up staunchly independent and thoroughly Australian in outlook—as the promotion of his Antarctic expeditions was to demonstrate. He

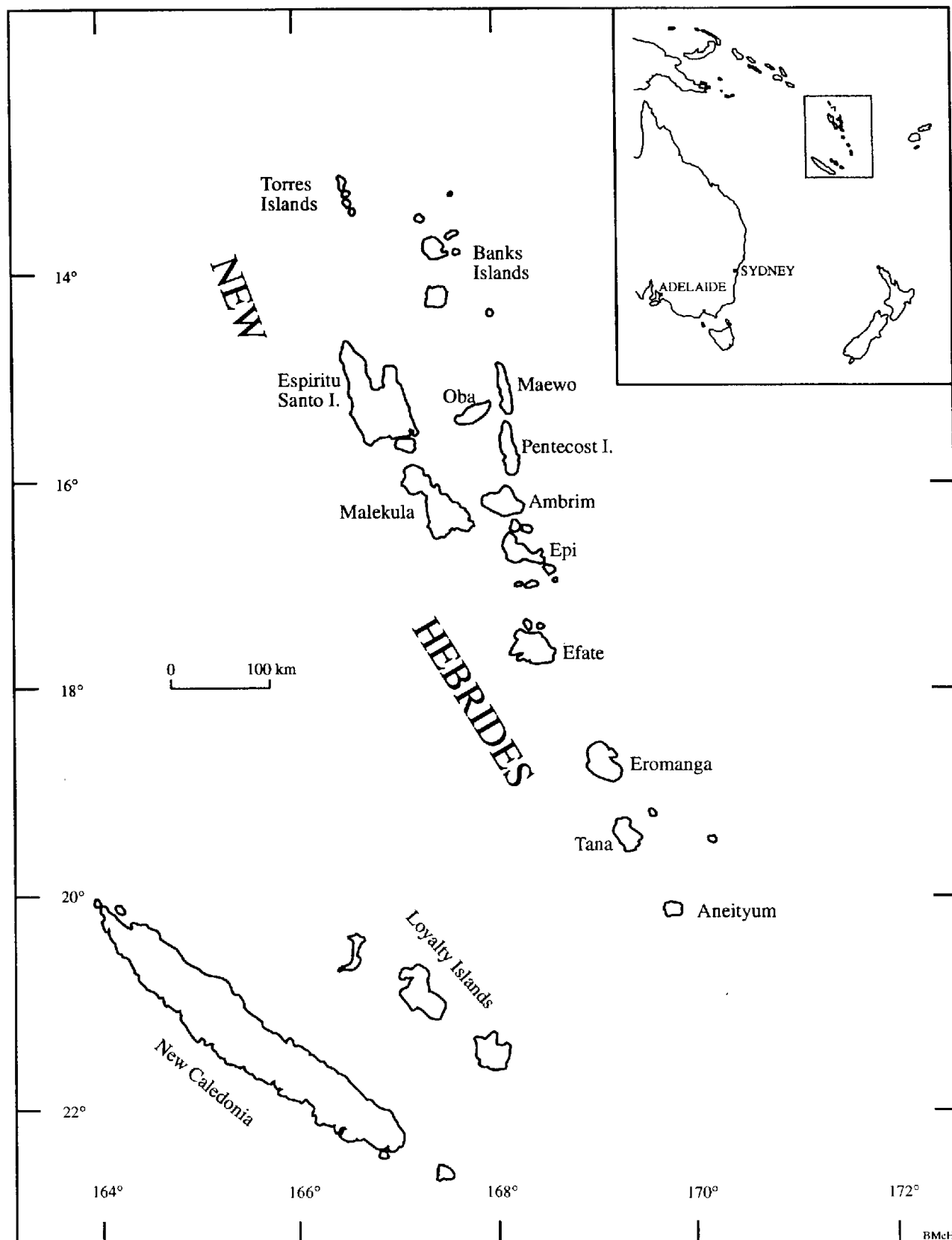


FIGURE 1. Locality map. The New Hebrides archipelago in the south-west Pacific.

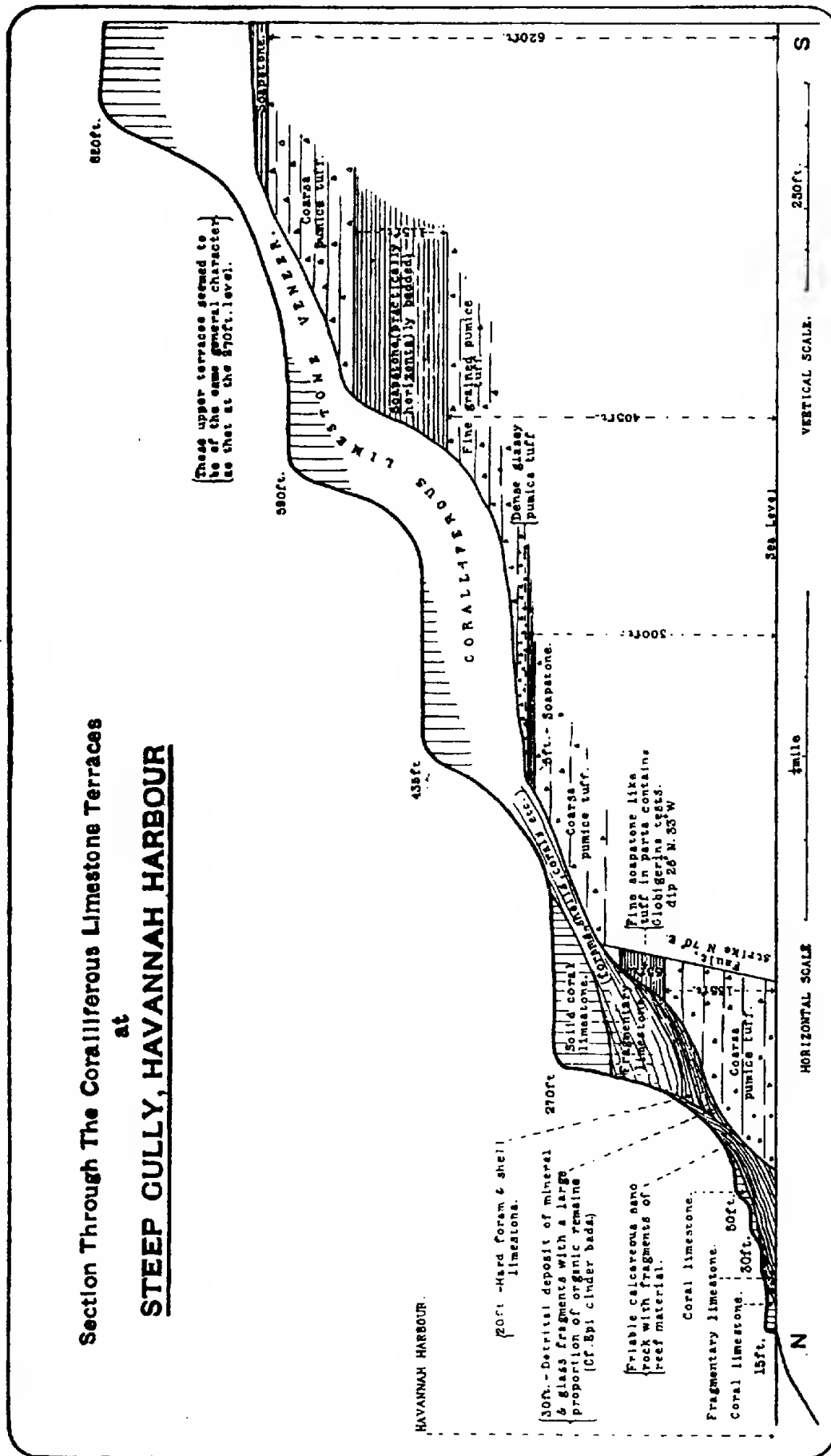


FIGURE 2. Mawson's stratigraphic cross-section of Eate. Proceedings, Linnean Society NSW 3, 1905.

entered the University of Sydney in 1899 at the age of 16, doing well in Physics, Chemistry and Mining on the way to his Bachelor of Engineering degree in 1901. But it was in geology that he excelled, gaining first class honours in 1900 and being awarded the petrology prize, and subsequently, in 1905, completing a B.Sc in geology. His inspiration came from the charismatic personality and the dynamic teaching of the Professor of Geology, T. W. Edgeworth David, who in turn was quick to recognise the abilities of the young science student. David was to become Mawson's mentor, fellow expeditioner and lifelong friend and confidant.

One of David's many preoccupations was ancient glaciation. As a young geologist in Britain he had followed with interest the debate on the nature of the latest (Pleistocene) Ice Age and the evidence of a much older glaciation (Permo-Carboniferous) discovered in India. Working for the New South Wales Geological Survey in the late 1880s he confidently identified glacial deposits in the Permo-Carboniferous rocks of the Hunter Valley. In 1901 he visited Mount Kosciusko where he immediately recognised the work of glaciers in the tarns, moraines and ice-sculpted valleys in the high country (David *et al.* 1901)—his views effectively settling a dispute that had continued ever since W. B. Clarke had reported evidence of glaciation there half a century earlier. Meanwhile in South Australia Walter Howchin had discovered glacial sediments, older than any known to that time, in the Sturt Gorge near Adelaide (Howchin 1901). These deposits (the Sturt Tillite) were assigned to the Cambrian but were later shown to be even older (late Precambrian), extending the evidence of past glaciation in both time and space and acting as a spur to the search for further clues to a former frigid earth.

David was Australia's first 'national' geologist, with interests spread well beyond his base in New South Wales. He had particularly strong links with South Australia through Walter Howchin, with whom he had collaborated in the field on such diverse matters as Cambrian fossils and glacial geology. It was perhaps inevitable that Mawson should become interested in these new developments which were extending the frontiers of Australian geology but his studies initially led him in other directions. In 1902 he was appointed Junior Demonstrator in chemistry and the following year he took six months leave of absence to make a trip to the South West Pacific.

The New Hebrides 1903

Mawson's first opportunity to explore and engage in adventurous fieldwork was due to the initiative and recommendation of David, who had a long-sustained interest in the geology of the Pacific basin. It was to prove a testing assignment for Mawson, requiring him to work under arduous and at times dangerous conditions, making the most of general short excursions from the ship as it sailed through the island archipelago, strung out over a vast area of ocean. Little known geographically away from the coastal fringe, the interiors were rugged and thickly covered with dense rainforest making access difficult while the native inhabitants had a reputation for being unpredictable and at times hostile.

Apart from a scanty record of previous investigations, the New Hebrides (Fig. 1) were a geological 'terra incognita' and for Mawson a challenge he was eager to meet: 'A great field was now open before us ... nothing has yet been gleaned as to the true nature of the rocks forming this extensive chain of islands'.

Mawson (and W. F. Quaife, a biologist) arrived at Vila, on the island of Efate and the chief town in the group on 13 April 1903. His first observations were made in the low hills around the town where a raised coral reef overlay volcanic sediments. This general geological situation was confirmed at locations further north along the coast where much thicker reef deposits overlay the 'foundation rocks'—a variable series of tuffaceous volcanics including agglomerates and pumice-rich beds (Fig. 2).

From Efate the ship steamed north to Malakula where Mawson wrote: 'The natives of Malekula are the most uncertain of any of the inhabitants of the group, having not yet abated from cannibal habits; indeed war was raging between the Natives ... at the time of our visit. For this and other reasons we were unable to examine this region very thoroughly'. Nevertheless he was able to make some investigations and excursions into the interior. Reaching Espiritu Santo, the largest island, a base was established at the mission settlement of Tangoa on the south coast and an assault made on Losumbuna (5 520 feet), the highest mountain in the New Hebrides. The interior mountains had never been explored by Europeans and the challenge was irresistible. Accompanied by three native guides, Mawson and Quaife negotiated two subsidiary peaks before bad weather, difficult terrain and, crucially, their guides' refusal to continue, forced a retreat.

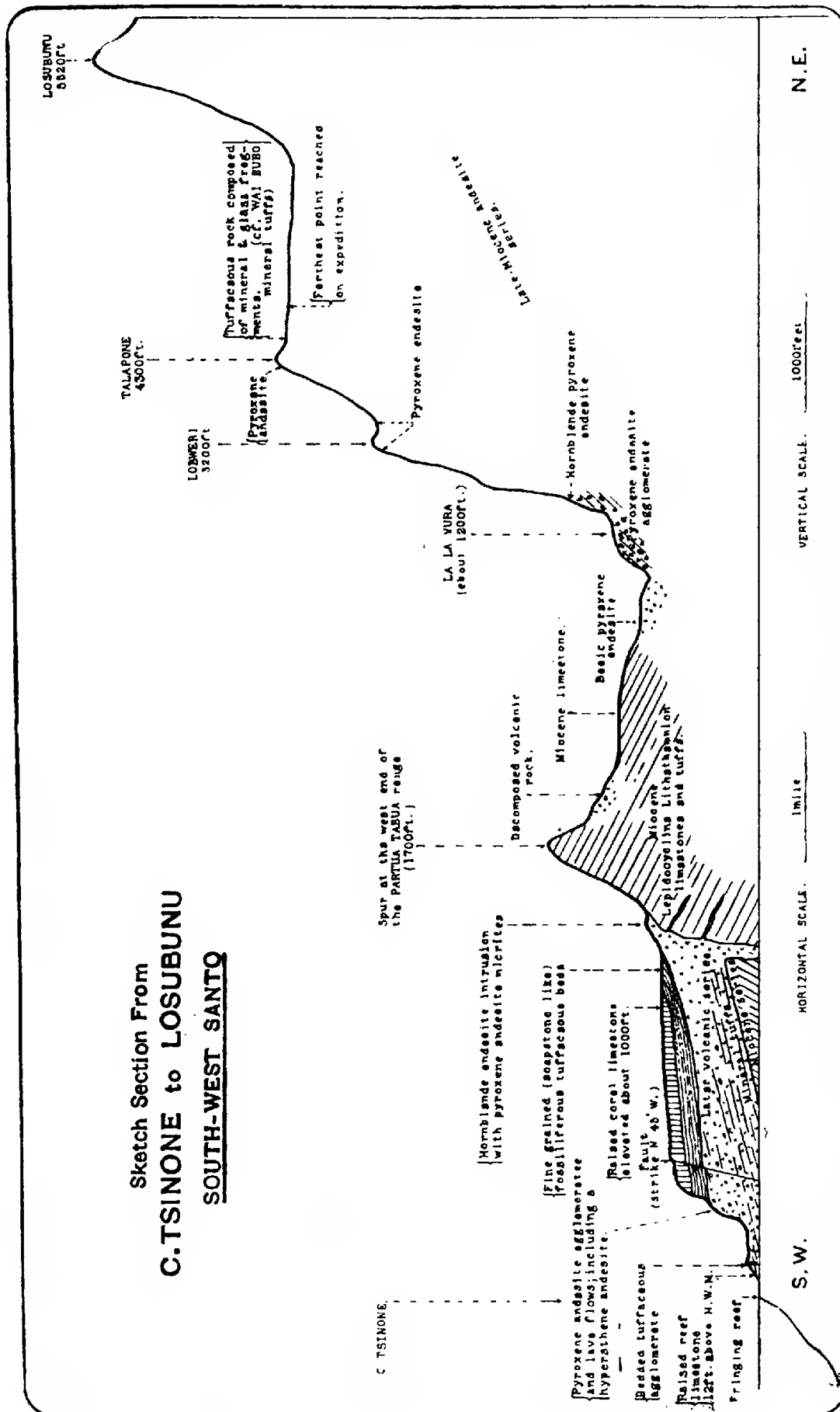


FIGURE 3. Mawson's section across Santo. Proceedings, Linnean Society NSW 3, 1905.

Although disappointed at not reaching their objective, Mawson collected specimens and made sketch sections of the rugged hinterland (Fig. 3). Fieldwork proved more productive along the coast where three separate pyroclastic units intruded by a variety of igneous rocks were found. An earlier report of older basement rocks (gneiss) in this part of the island could not be confirmed despite diligent searching.

The northern-most islands in the chain were covered in a cursory reconnaissance, but enough to confirm the volcanic nature and essentially basic composition of the Banks Group. Arriving back in Vila in mid-August after four months away, the expedition was greeted by a minor earthquake with another tremor following a few days later—enough to indicate the seismic instability of the region. Finally, investigations in the Havannah Harbour area provided key sections in the local sequence of volcanic sediments and overlying reef deposits.

The New Hebrides expedition was inevitably very much a reconnaissance and Mawson was keenly aware of the limitations of his survey. One of the strengths of his published report (Mawson 1905) was his inclusion of all previous references, both published and unpublished, to the geology and physical features of the islands. The general seismicity of the region, already well documented, and which Mawson himself experienced, he attributed to local volcanic sources, recognising also the importance of regional tectonic movements along major faultlines. He wrote: 'before long numerous seismological stations will be distributed through the South Pacific Islands, as only by analysing such data as would result, can definite decisions regarding the present earth-movements in this much-troubled area be arrived at'. It was to be fifty years before that hope began to be realised.

An anticipation that because the old rocks of nearby New Caledonia were mineral-rich, the New Hebrides might be similarly endowed was quickly dispelled because of the geological youthfulness of the islands. Sulphur deposits and iron-bearing sands were the only resources considered to be of possible future commercial value. Within the regional context of the Pacific basin, Mawson viewed the New Hebrides island arc as of late Tertiary age, one of a series of parallel arcs which were remnants of a much fragmented continental mass. Folding and over-thrusting, associated with volcanicity, against a rigid foreland lying to the west (New Caledonia), had been followed by major faulting and sea-floor subsidence.

The evidence for elevation which most impressed Mawson were the raised coral reefs. These capped the Tertiary deposits and ranged in terraces rising to over 2 000 feet (609 metres). They were estimated to be post-Pliocene in age, and gave a clear indication of continued tectonic activity since the middle Tertiary.

His published account of the New Hebrides expedition put the islands on the map geologically and established Mawson as a resourceful and perceptive field worker, competent in many areas of geology and with a flair for synthesis. He foreshadowed many of the more recent interpretations of south-west Pacific region geology made in the light of Plate Tectonic theory, with the New Hebrides viewed as an island arc of volcanic lavas and pyroclastic rocks and intrusions adjacent to a deep ocean trench and above a steeply dipping seismic zone.

Early Researches

On returning to the University, Mawson was soon involved in research (with fellow student and later Antarctic explorer Griffith Taylor) on the igneous rocks in the Bowral-Mittagong area, south-west of Sydney. The Mittagong study (Taylor and Mawson 1903) was the first of many on the petrography and petrology of igneous rocks in their regional setting which was to remain a prime interest in the years ahead. About this time Mawson also began investigations into the radioactive properties of minerals. This was a pioneer study in Australia, closely following the discovery of radioactivity by Becquerel in 1896 and the follow-up work by the Curies which led to the isolation of radium in 1898 and the recognition that uranium and thorium-bearing minerals were radioactive. Mawson reviewed these recent researches and carried out tests on natural waters, mud, soil and air. He was required to construct his own analytical equipment, notably a gold-leaf electroscope, and a large number of Australian minerals was tested including the only two known occurrences of uranium-bearing minerals in Australia and which gave the predicted high readings. The other minerals found to test positive were mainly monazites from various tin-fields around Australia. His short paper (Mawson & Laby 1904) marked the beginning of a life-long interest in the geological occurrence of radioactive minerals and their economic potential.

South Australia 1905

Late in 1904, Mawson, with the support and encouragement of David, was appointed to the position of Lecturer in Mineralogy and Petrology at the University of Adelaide. He arrived to take up his academic duties full of enthusiasm and with high expectations but was immediately confronted with a lack of suitable accommodation and facilities for geology due to the University's chronic shortage of funds. Frustrations developed which were to dog him for many years, including the necessity to forge a working relationship with the only other member of the Geology Department, Walter Howchin. Already with an established international reputation and with a great deal of experience of South Australian geology, Howchin was 60 years of age when Mawson, 23, arrived on the scene. It seems there were tensions from the start. The question of 'spheres of activity' (Mawson's phrase) provided an immediate and ongoing irritant, to be temporarily removed when Mawson went south in 1907.

The geology of South Australia was known in broad outline at the beginning of the century (Corbett *et al.* 1986). This was due predominantly to the work of three men: Ralph Tate, the first geologist appointed to the University (1875–1901); Walter Howchin, Methodist Minister and enthusiastic amateur until his appointment to the University after Tate's death in 1901; and H. Y. L. Brown, the first Government Geologist who was to act as a one-man Geological Survey from 1882 until 1912. While Tate and Howchin worked mainly, though not exclusively, close to home in the Mount Lofty Ranges, Brown had been carrying out some epic geological explorations in the northern regions of the State which at that time included the Northern Territory. He published the first geological map of South Australia in 1883, revising it periodically. His 1899 map was a remarkable achievement and in its essentials remains little changed today.

Tate had discovered glacial features at Hallett Cove in 1877; Howchin subsequently demonstrating the widespread evidence for this glaciation outside the Adelaide region and establishing a Permo-Carboniferous age for the event by about 1900. In 1901 Howchin, as mentioned previously, had discovered the much older glacials in the Sturt Gorge, a few miles south of Adelaide. But perhaps the most significant of all the early breakthroughs was the finding of Cambrian fossils in the old rocks on the western flank of the Mount Lofty Ranges

(Howchin 1897). Howchin thereafter concentrated much of his effort on determining the stratigraphy of the western ranges.

It was Howchin's clearly expressed 'prerogative' to work in most areas of the State that prompted Mawson to choose the remote Olary-Broken Hill area for his first extensive field investigations. It was a decision both judicious and timely. Not only did this work extend Howchin's researches on the supposed Cambrian rocks of the Mount Lofty Ranges into the Olary Spur and over the border to Broken Hill and the Barrier Ranges, but the problems presented by the region also satisfied his interests in mineralogy, petrology, and stratigraphy and his discoveries were to influence his future involvement with glacial deposits both ancient and modern.

The explorer-geologist was severely tested in the harsh environment near the north-east state border. It was (and is) an arid, inhospitable and sparsely inhabited country. Previous investigations had centred on and around the Broken Hill ore-body itself—the largest silver-lead ore body in the world. While little was known of the origin of the ore-body and its stratigraphic controls, Mawson set himself the task of ascertaining the broader regional context of the deposit. His methods involved covering the ground in a series of traverses on foot, horseback, bicycle and on occasions, by motor vehicle. He was to determine and define two major rock divisions in the Olary-Broken Hill region:

1. An older basement complex of metamorphic rocks including gneiss, schist, amphibolite and granite of Precambrian age which he named the *Willyama Complex*, and
2. A younger series of sedimentary rocks, in part metamorphosed, of assumed Cambrian age including a wide variety of rock types, the most notable and persistent being boulder-beds and related sediments of glacial origin. This he named the *Torrowangee Series*.

In January 1907, the Australasian Association for the Advancement of Science (AAAS), held its meeting in Adelaide and Mawson gave two (unpublished) papers based on his recent field work and particularly concerned with the glacial beds. His interest in these beds and a desire to reach a full understanding of their nature and origin was developing rapidly. Many years later he wrote to Edgeworth David that his commitment to glacial geology dated from December 1906 when his Olary field investigations were well underway. Matters moved very rapidly at the end of 1907. Mawson heard, through David (who was

to join the British Antarctic Expedition), that the leader, Ernest Shackleton, was to visit Adelaide briefly on his way to New Zealand to join the 'Nimrod'. Mawson successfully requested a meeting and volunteered his services for the summer season. Within three days Shackleton had offered Mawson the position as physicist for the duration of the expedition. The opportunity to realise his ambition to experience 'an ice-age in being' was too good to miss. He accepted, quickly arranging for a 'locum' to cover his absence from the University, and left Adelaide before the end of December bound for the Antarctic.

South With Shackleton – the British Antarctic Expedition

David was senior geologist on the expedition with Raymond Priestley, a young man with no formal qualifications in science, as his deputy. Mawson as physicist had no official role in this area. Yet from the start David involved his old student in the geological program and in two of the three main journeys undertaken by the expedition—the ascent of Mount Erebus and the trek to the South Magnetic Pole. Mawson played a crucial role, both as a young and vigorous team member and a valuable contributor to the geological work, which David was quick to acknowledge in his final report (David & Priestley 1914). Here Mawson is referred to as Mineralogist, Chemist and Physicist to the expedition (the study of Antarctic ice—its crystallisation, granulation and other properties—was considered by David as much a matter of mineralogy as of physics). The report incorporates much of Mawson's thinking and his contribution to it was wide-ranging, covering mineralogy and petrology and stratigraphy, as well as economic geology implications and broad-scale considerations of Antarctic geology within a global context.

Mawson and David were both in the small party which reached the summit of Mount Erebus (3 794 m) on 8 March. Mawson made a traverse map of the eight day journey which provided its share of adventures (Shackleton 1911). He also took photographs and collected rock specimens. Later that winter (June 14) the volcano was seen in eruption from their base, steam issuing from the crater, although no lava was observed on the flanks of the cone.

With the coming of spring, preparations were made for the two major assaults of the expedition;

Shackleton's push for the geographic pole and an attempt by a northern party (David, Mawson and McKay) to reach the South Magnetic Pole. The route was along the coast of Victoria Land as far as the Drygalski Glacier Tongue, where they were to turn inland climbing onto the Polar Plateau towards the pole. A general survey of the geology of the coast and where possible of the Western Mountains was an important part of the program. The early stage of the journey was along the edge of the sea-ice with outcrops confined to occasional rocky bluffs projecting from under the ice-cap. Observations were made at Cape Bernacchi (marble), Cape Irizar, Granite Harbour and Depot Island. The rocks encountered were highly altered (metamorphic) and included gneiss and schist together with granite (itself metamorphosed) and basic lavas. Looking inland through field-glasses, these lavas were seen at a higher level to overlie the granites and in turn to be succeeded by stratified rocks which were taken to be the Beacon Sandstone, discovered and described by Ferrar (1907) on Scott's first expedition (1901–03). David described Depot Island as '... most wonderful geologically and a perfect elysium for the mineralogist'. Mawson relished the variety of rocks and minerals they found, among them epidote, pyrite, copper pyrites (chalcopyrite), garnet and manganese oxides, some of which he thought might prove of economic value. Certain of the rocks, notably the gneiss and granite reminded him of those in the Broken Hill area. Meanwhile the ubiquitous glacial debris (moraine) dumped at the melting ice-front was a rich source of supplementary evidence of what lay further inland, below the ice-cap. Erratics at one locality were very similar to the Victor Harbor Granite.

The ascent of the plateau became an ordeal and any thoughts of geology were replaced by concentrating on the dash for the magnetic pole. The elusive and ever-wandering point was reached on 16 January 1909. The return journey proved a battle for survival and the party was very fortunate to make the rendezvous with the 'Nimrod' and safety.

The information collected by the Magnetic Pole party made a valuable contribution to the geological results of the expedition. Notably, David and Mawson were able to build on Ferrar's earlier work and show that Victoria Land comprised a basement complex of metamorphic, igneous and mineral-rich rocks of assumed Precambrian age, overlain by a sedimentary sequence, which, on the limited evidence available, included rocks intermediate in age



FIGURE 4. Mawson, seated, on his return from Antarctica, 1909. Howchin stands at his right shoulder. Photo. P. Driver-Smith.

between the basement and the Beacon Sandstone.

For Mawson the expedition proved a stimulating and scientifically rewarding experience. His desire to experience modern glacial processes in action had been achieved and the insights gained were to be developed on his next journey south and later applied to the ancient glacial deposits of South Australia. Above all, his participation in the Shackleton expedition had determined his lifelong interest in the southern continent.

Interlude

Mawson returned to Adelaide in April 1909 to a hero's welcome (Fig. 4), but within a few weeks he was back in the Olary–Broken Hill country, hiring a horse and dray and continuing his investigations among the mineralised rocks and the ancient glacial beds of the arid north. After completing his fieldwork, he spent some time in Broken Hill writing up his results, and on laboratory studies of the mineralogy and petrography of the key rock types. He was particularly impressed by the pegmatites which were such a prominent feature of the region and wrote: 'In no other part of the world can pegmatite formations occur on a more extensive scale'. The

study of pegmatites was at that time in its infancy and Mawson recognised that in Olary he had evidence of their importance as 'a connecting link between the igneous rocks and the differentiated products economically worked as ore deposits'. His fieldwork, and the subsequent published review (Mawson 1912a; Fig. 5) of all aspects of the geology and economic geology of this important and yet little known mineral province, was a major contribution to South Australian geology and earned him the degree of D.Sc. from the University of Adelaide in 1909.

While in Broken Hill he examined and valued several mineral collections from the mines on behalf of the South Australian Museum. Some of them included specimens of outstanding quality. Mawson had first acted for the Museum in 1906, when he had successfully acquired the Dunstan Collection from the Wallaroo Mines. In 1908 he was appointed Honorary Curator of Minerals, thus beginning a long and productive association with the Museum which was to last his lifetime, and which became crucial in later years, as no full-time curator responsible for the collection was appointed until 1956. The Mawson-Museum connection cannot be treated in any more detail here.

Early in December 1909, Mawson left Adelaide for London on board the SS 'Mongolia'. He was

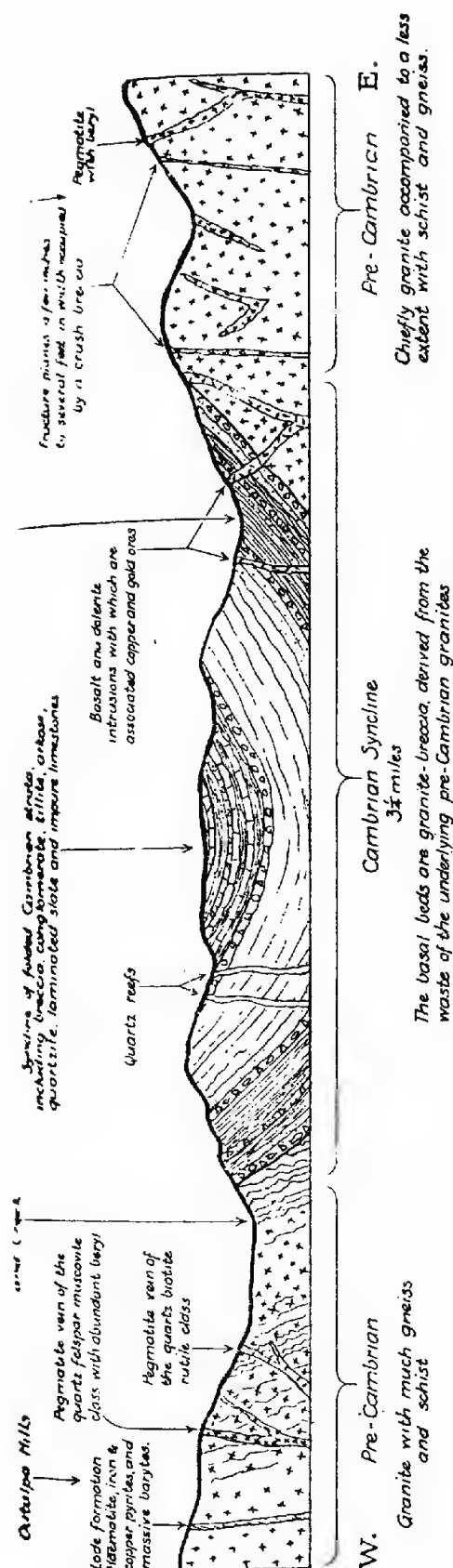


FIGURE 5. Mawson's interpretation of the geology near Olary, South Australia (1912b). Courtesy ANZAAS.

keen to go to the Antarctic again and full of ideas for a scientific program that he hoped would appeal to either Shackleton or Scott, both of whom he knew had plans for expeditions south. Scott was very keen to enlist Mawson (even offering him a place in the final polar party), but was not prepared to consider any modification of his own plans which were already well advanced. Discussions were long and frank but when Mawson learned that the position of chief scientist (which he might have accepted) had been filled and his proposal for a western party to explore King George V Land unacceptable, he declined Scott's offer. He was simply not prepared to compromise his purely scientific approach to Antarctic exploration. As for Shackleton, initially Mawson maintained friendly relations with his former leader, even visiting a gold prospect in Hungary which Shackleton was convinced would make his fortune (and Mawson's too if he came in with him as an investor). But becoming increasingly disillusioned with Shackleton's erratic behaviour and lack of firm plans, Mawson followed him to America in an attempt to pin him down; and the two signed an agreement that an expedition would leave late in 1911 and should Shackleton be unavailable as leader Mawson was to take over and receive all Shackleton's support and assistance in raising funds. Ever the realist, it was clear to Mawson that the responsibility for mounting the expedition was most likely to be his and so it proved. He was then faced with the daunting task of raising funds quickly and in competition with Scott who had a head start and the advantage of being based in London. Mawson returned to Adelaide. For the next eight years the Antarctic was to dominate his life. But for a brief interlude he returned to academic life and his research activities and to these we now return.

Radioactive Minerals: Radium Hill and Mount Painter

Mawson's involvement with radioactive minerals had been renewed soon after his arrival in South Australia when in May 1906 carnotite, a highly radioactive mineral, was found in ore taken from a mine 24 miles east-south-east of Olary. H. Y. L. Brown visited the site and issued a report in which he speculated that the mineral was a decomposition product of primary uranium ores occurring at depth. In August, Mawson obtained samples which he passed over to E. H. Rennie, Professor of Chemistry, for analyses which

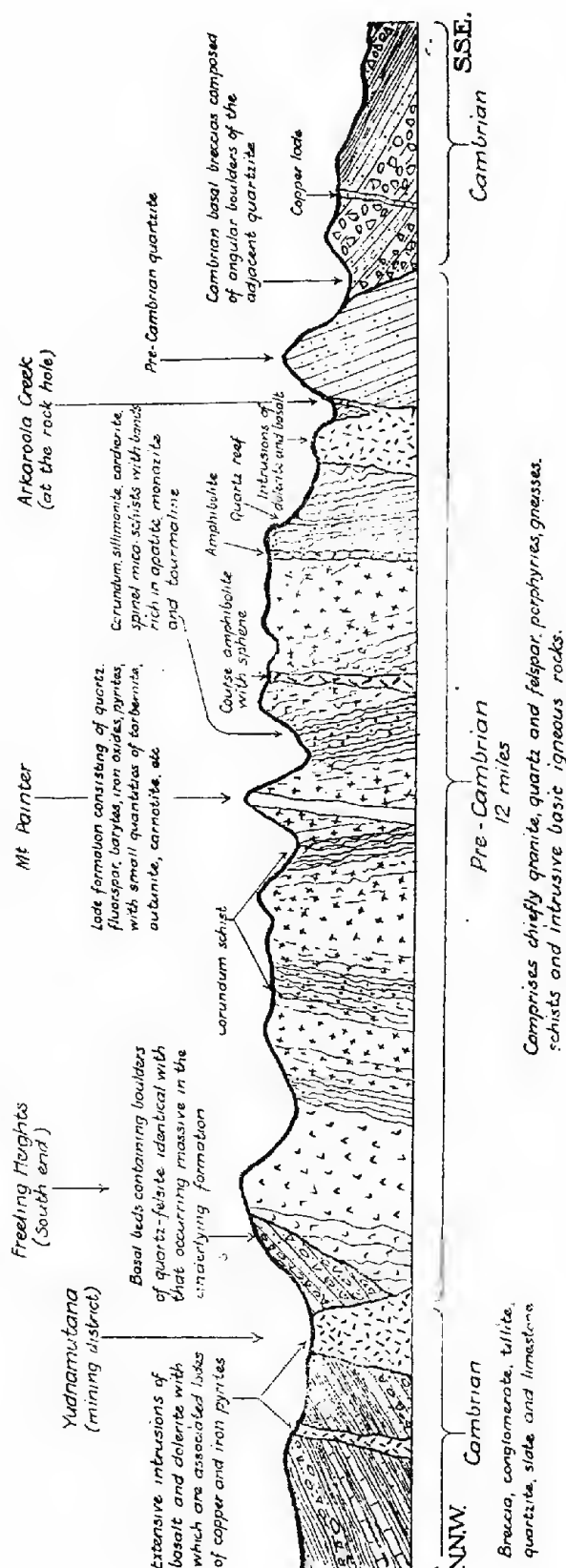


FIGURE 6. Geological cross-section in the Mt Painter - Arkaroola area (1912b). Courtesy ANZAAS.

suggested that black minerals initially identified as magnetite, were far more complex. This prompted Mawson to visit the mine and make a detailed survey of the exposed reefs which had been pegged originally in the belief that the prominent black mineral was a tin-bearing ore. Further examination showed that while the magnetic iron/titanium mineral was dominant in the main reef, a rarer black mineral with a distinctive and very brilliant lustre also occurred as grains, streaks and cubic crystals. Analysis shows that in addition to a high percentage of iron and titanium the mineral also contained rare earth elements together with uranium, vanadium and chromium. Mawson proposed the name Davidite for what he believed to be a new mineral species in honour of his former teacher (Mawson 1906). He also identified Roscoelite, a bright green vanadium-bearing mineral. At a time when knowledge of radioactive minerals was in its infancy, Mawson recognised the deposit as a significant discovery, possibly of economic importance, and named the locality Radium Hill. He was optimistic but cautious in his appraisal: 'This body of radio-active ore is, in the matter of quantity, much the most important yet discovered in Australia. Its low grade, however, introduces serious difficulties to commercial enterprise in this direction'. Radium Hill was to have a long but intermittent history based on the working of its radioactive lodes (Fig. 7), and Mawson was to renew his interest in the deposit in the 1920s.

Mawson visited the Flinders Ranges for the first time towards the end of 1910, during his short spell in Adelaide between Antarctic expeditions. He had received a visit from W. B. Greenwood, the owner of Umberatana Station, who had brought some specimens of a bright green mineral which Mawson identified as torbernite, an hydrated phosphate of copper and uranium. Greenwood had been prospecting in the northern ranges on behalf of the Mines Department for several years and had become annoyed when specimens, including the green mineral, which he had left at the Department some time before had not received attention; whereupon he had retrieved them and taken them to the University. Excited by the prospect of another radioactive mineral deposit in South Australia, Mawson headed north and, with Greenwood and renowned prospector Harry Fabian, made an examination of the geology and mineral occurrences in this most rugged and inaccessible part of the Flinders, attempting to place the local geology in the broader regional context (Fig. 6). The short visit marked the

beginning of his long and fruitful association with the geology and mineral resources of the region and his field notebook for the trip is full of detail of his observations and the excitement of discovery; for example: 'The results of my recent journey have been in the highest degree satisfactory... My main objective was the investigation of the metamorphic rocks eastward of Yudnamutana in connection with the interpretation of the Barrier Ranges, a subject in which I have long been absorbed...'

With regard to the potential of the uranium-bearing lodes he wrote: '... the outcrop is on the whole low grade, though richer patches are met with at intervals. Improvement may be expected below. The ore can be treated very inexpensively and this will offset the low-grade character. So far as I am aware this is the most extensive uraniferous lode formation in the world'. The back of his field notebook contains estimates of costing for ore extraction, transport, freight and handling, including comparisons for treatment on the spot, at Port Pirie or in England. There would be a need for roads and wells and for camels to bring out the ore. If the grade proved high enough, he foresaw the setting up of a company to work the ore—the Radium Extraction Company. He even worked out the capital required – £20 000. These estimates may have been doodlings around the campfire, at the latest they were put on paper soon after his visit, and they have an immediacy which reveal Mawson's keen interest in the region, its economic potential and his desire to be part of the action. He was not to return north for more than a decade. Over the next few years some intermittent mining activity took place at Mount Painter, but with the outbreak of World War I activity ceased.

South Again – The Australasian Antarctic Expedition (AAE) 1911–14

In January, 1911, Mawson gave a lecture to the combined geology and engineering groups at the annual meeting of the AAAS in Sydney. It was a fund raising exercise designed to appeal to national pride as well as pointing out the scientific and future economic potential of the southern continent. He stressed that: 'the collection of scientific data (was) obligatory upon us ... its mountains were blessed with mineral resources ... (and) it holds among its fossil strata secrets especially interesting to Australians'. Science was to be linked to technology and the latest developments—the wireless and motor sledges—

still to be tested down south, were seen as a vital aid to scientific exploration. The burdens of leadership were enormous leaving little time for any geological researches of his own, but Mawson recruited a strong team of four geologists who were to carry out valuable surveys over a great expanse of territory. Cecil Madigan, later to join his leader at the University of Adelaide, was appointed meteorologist.

Reaching the area selected for the expedition's base, the expedition ship 'Aurora' had great difficulty in breaking through the ice barrier and was forced to cruise westward; Mawson had hoped to find the Antarctic continent in these latitudes bounded by a rocky and attractive coast like that in the vicinity of Cape Adare, the nearest well-explored region. The poor prospects of carrying out extensive geological work under such conditions must have been a blow, but Mawson was impressed and awed by the sheer physical presence and power of the ice and its dominance of the environment: 'The land was so overwhelmed with ice that, even at sea-level, the rock was all but entirely hidden. Here was an ice-age in all earnestness; a picture of northern Europe during the Great Ice Age some fifty thousand years ago' (Mawson 1915, 1996 p. 40).

The main base was established at Cape Denison (Commonwealth Bay) and a western base party, including two geologists, some 1 500 miles (2 400 km) further along the coast to the west on the edge of the Shackleton Ice-Shelf. The vicinity of Cape Denison was comparatively ice-free, and the geologists were able to study glacial erosion and deposition at first hand. The rocks outcropping near the main base were predominantly metamorphic—folded and contorted gneiss and schist of presumed Precambrian age. Evidence of ore-bearing minerals was also found, among them iron, copper and molybdenum which Mawson believed gave promise of larger bodies in the vicinity and indicated the probability of mineral wealth beneath the continental ice-cap. Around the edge of the ice margin, the terminal moraines were 'a veritable museum'. Rocks, showing every variety in colour and form, were assembled, transported from far and wide over the great expanse of the continent ... 'The story of the buried land to the south is in large measure revealed in the samples brought by the ice and so conveniently dumped' (Mawson 1915, 1996 pp. 74–76). After a particularly severe winter with hurricane force winds, the summer journeys commenced, and much valuable scientific work carried out. A western party made a particularly

interesting find, the first meteorite from Antarctica, duly named the 'Adelie Land Meteorite', and the first of many to be found in later years.

Mawson himself, with Ninniss and Mertz and the dogs, set off on the longest and most ambitious of all the journeys, striking east on a southerly course in an attempt to cover as much territory as possible in the time available. The story of that harrowing journey which cost the lives of both of Mawson's companions, and of his miraculous return against overwhelming odds just in time to see the 'Aurora' disappear over the horizon, is an epic story of endurance, fortitude and sheer will power which has been well told by Mawson himself in 'The Home of the Blizzard' (Mawson 1915) and by Bickel (1977). Mawson and the small remnant of the expedition left behind to search for him had to face another Antarctic winter. The 'Aurora' returned in December 1913 and on the 26 February 1914, Mawson arrived back in Adelaide.

The War Years and After

The expedition was home, but for Mawson there was to be no respite and it was to be a further six eventful years before he was able to resume an ordered academic life again. The First World War began as he was returning from an overseas business trip to Europe concerned with the wind-down of the expedition, and by 1916, after travelling to the United States, he was back in Britain where he spent the remainder of the war on highly responsible government work with the Ministry for Munitions. He did not return to Adelaide until May 1919. Back at the University he found that little had changed in his absence except that Walter Howchin had been awarded the title of Honorary Professor in Geology and Palaeontology in 1918. Mawson (1944a) wrote later: 'I was not a little confounded. I would have packed up and left immediately but for the supreme consideration of faithfully recording and adequately publishing the immense mass of data received during my Antarctic Expedition'. Early in 1920 he talked with Howchin about the future: 'stating that I was not prepared to continue at Adelaide for another year under the then existing inadequate arrangements for geology'. There was no prospect of the much-needed new building for geology and Mawson tied himself to a compromise twenty year agreement on additional accommodation which proved increasingly

inadequate as years went by, and which he was later to regret. Meanwhile, Howchin's continuing presence at the University was perceived by Mawson as a hindrance to the satisfactory development of the Geology Department and it must have been a great relief to him when Howchin, then 75, decided to retire at the end of the year.

In 1921 Douglas Mawson was appointed to the newly created Chair of Geology and Mineralogy, and Dr Cecil Madigan, his old comrade from the Antarctic, joined him as Lecturer the following year. Mawson and Madigan were to be the only two staff members in the Geology department for much of the inter-war period. The establishment of the new department and his teaching and administrative duties (not to mention continuing Antarctic matters) took precedence in the early 1920s but field investigations were resumed in both the Olary region and the north Flinders Ranges. While he built on his work in the Boolcomatta area, locating several key sections spanning the junction between the basement and overlying sedimentary sequence, he was never to resume a sustained fieldwork program in the region, despite the urgings of David.

David's retirement at the end of 1923 and the politics involved in choosing his successor proved unsettling for Mawson who at that time was still not fully committed to staying in Adelaide and applied for the job, and although the best qualified of the candidates, he was ultimately unsuccessful because of David's influence on the course of events and his (perhaps over-zealous) loyalty and support to Leo Cotton, his deputy and locum for many years, who was appointed to the Chair. The outcome certainly posed strains on the David-Mawson relationship, and further tensions and distractions were to follow when David's increasing obsession with the search for supposed Precambrian fossils focussed on the old rocks in South Australia (see also p124, End of an Era). On an earlier visit to Adelaide in 1921, David had found what he believed to be arthropod remains in the old rocks at Reynella (long considered by Howchin as Early Cambrian) tentatively placing them in the late Precambrian (Proterozoic) and proposing a new division - the *Adelaide Series*.

Meanwhile, Mawson turned his attention to the north Flinders once again. He had published a brief comparison of the Mount Painter and Olary provinces (Mawson 1912b), but the results of his investigations around Mount Painter in 1910 were treated more fully in a long-delayed paper (Mawson 1923) in which he recognised a core of



FIGURE 7. The Radium Hill Mine, soon after its discovery. Mawson, 1944b, pl.19. Courtesy Royal Society of South Australia..



FIGURE 8. Mount Gee, viewed from the west. Mawson, 1944b, pl. 19. Courtesy Royal Society of South Australia.

Precambrian igneous and metamorphic rocks overlain by a sedimentary series similar in many respects to those overlying the basement in the Adelaide region. He followed David's lead in applying the term *Adelaidean* (Adelaide Series) to these sediments and suggesting a Proterozoic (late Precambrian) rather than Cambrian age. Igneous activity included two acid phases, the second with pegmatites and aplites followed by a volcanic phase characterised by vesicular basalts. The mineralisation of the Mount Painter-Mount Gee area, notably the quartz reef at Mount Gee and the uranium minerals (torbernite and autunite) at Mount Painter, was described in detail (Fig. 8).

Following Mawson's enthusiastic report on the uranium potential of the area after his initial visit in 1910, several companies had been floated and prospecting carried out on Radium Ridge and Mount Gee. Meanwhile the Mines Department had been more cautious but in favour of further prospecting. Sporadic attempts at developing the prospects (notably the No. 6 workings) had

languished during the war, but in 1924 there was renewed interest in radioactive ores world-wide and a return to the Mount Painter field seemed justified. Consequently, Mawson returned north in November 1924 and spent much of his time in the Mount Painter area on detailed study of the mineralised rocks but also in broader scale assessment of the regional context of the mineralisation.

The regional geology of the Flinders Ranges was little known at this time. Howchin had made a pioneer traverse from west to east at the level of the Parachilna Gorge in 1907 but the results were not published until 1922. While on his return trip from the north, Mawson had the good fortune to make a particularly significant discovery just west of the Italowie Gorge. It was a case of the prepared mind recognising the significant evidence and provides a good example of Mawson's versatility as a geologist, for fresh from the mineral riches of the Mount Painter country he was now to show that he had a good eye for a



FIGURE 9. Entering Yudanamutana. Mawson, 1923, pl. 33. Courtesy Royal Society of South Australia.

fossil also. What he found were 'curious markings' on roadside outcrops of limestone which 'on inspection ... was found to be due to massed fossil heads of a *Cryptozoon*-like alga ... developed in a massive formation, the algal remains constituting the bulk of at least some of the beds' (Mawson 1925). Similar structures had been reported from the MacDonnell Ranges by Chewings and described by Howchin (1914) but there was as yet no general agreement on their stratigraphic position. Mawson inclined towards an Early Cambrian age, but David, on hearing of the find thought they might be older (Proterozoic). Very little was then known of Precambrian life forms; most of the obscure remains described being referred to as *Cryptozoon* (hidden life)—but the recently announced discovery of algal fossils in Precambrian rocks in Montana by Walcott suggested that the Flinders rocks might be of similar age. David certainly believed so and urged Mawson to investigate further. Mawson's

'Cryptozoons' are now recognised as algal stromatolites. These columnar and dome-shaped structures produced by the trapping of sedimentary particles by mats of blue-green algae are the earliest abundant fossils and are well developed in certain of the Precambrian rock formations in the Flinders Ranges. Mawson, however, was not to be pressured into narrow specialisation and continued his wide-ranging investigations of Flinders Ranges geology (Figs 9, 10), publishing further papers in the mid 1920s. One was on the volcanic rocks of the Wooltana area (Mawson 1926a), first encountered in Arkaroola Creek in 1910 and subsequently examined near Wooltana on a brief visit in 1924. There he found a thick sequence of volcanics—vesicular lavas, tuffs and agglomerates overlain by boulder beds and finer sediments which he described as: 'most probably of fluvio-glacial and glacial origin'. Large granite boulders higher in the section were even more convincing, leaving: '... no doubt in my mind ... as to the glacial nature

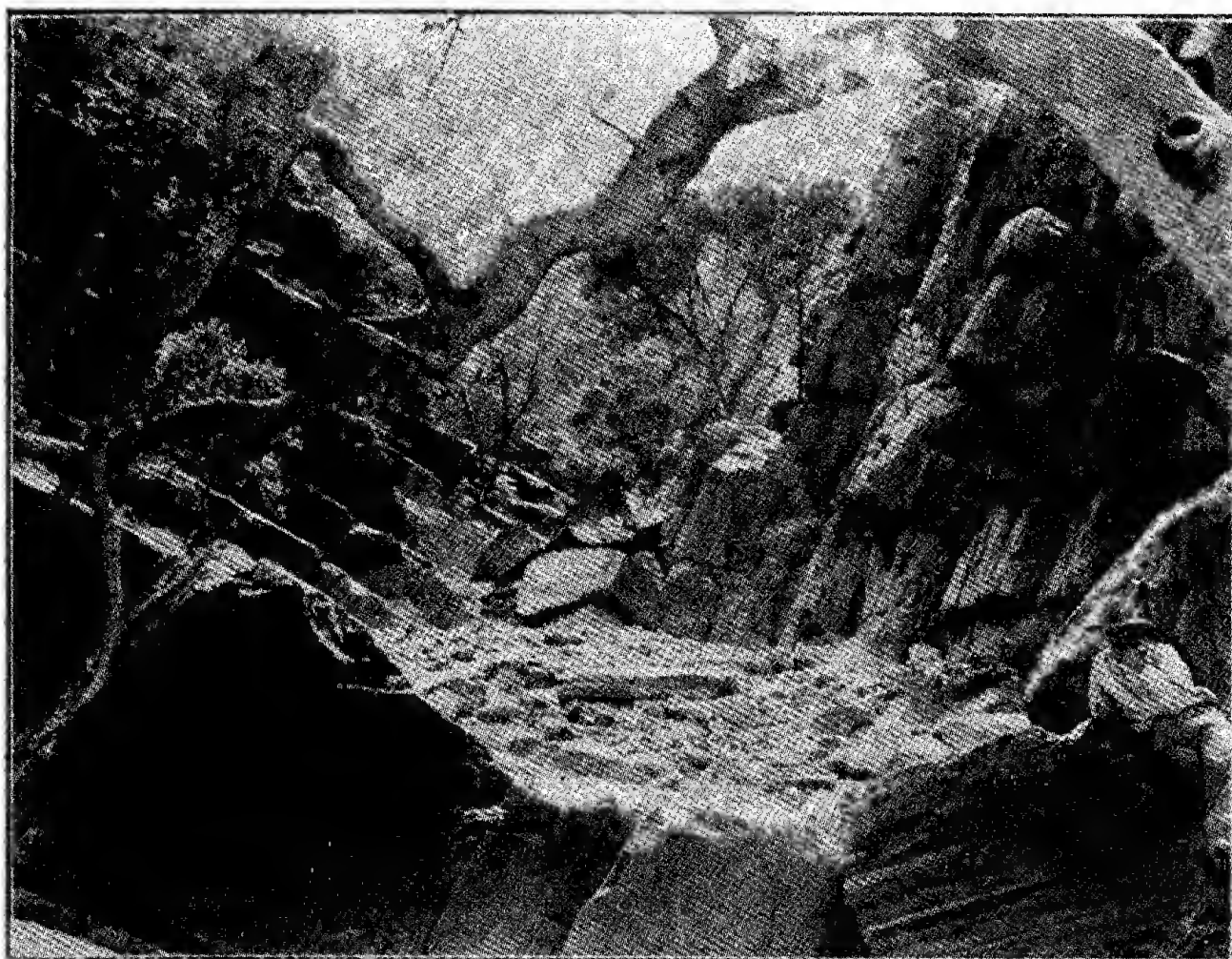


FIGURE 10. The quartzite of the Yudanamutana Gorge. Mawson, 1923, pl. 33. Courtesy Royal Society of South Australia.

of these beds...’ Sediments above the glacials, unsuccessfully searched for fossils, were believed of likely Late Precambrian age.

Another spin-off from the 1924 North Flinders trip was a visit to the Paralana Hot Springs which interested Mawson because of the radioactive nature of the waters (Mawson 1927a). For a short period about this time an enterprising doctor had sought to capitalise on the supposed therapeutic qualities of the spring by setting up a spa on the site, although with no success. The springs are situated close to the faulted junction between the old rocks of the ranges and the younger sedimentary basin to the east. While most geologists supported an origin from deep-seated basin waters, Mawson speculated on a possible contribution from the highly uranium-rich rocks lying to the west. He collected water and gas for examination, hoping the latter would prove rich in helium. Unfortunately the samples did not survive the journey back to Adelaide. The highly active gas which at first puzzled the analysts, has since proved to be rich in radon; the water is much less radioactive.

Mawson had made a brief visit to the Willouran Ranges on the north western flank of the Flinders in 1920. From here he described and named the *Willouran Series*—a thick sequence of sandstones, slates and calcareous beds underlying a dominant quartzite formation and forming a synclinal structure (Mawson 1927b). Sediments of probable fluvio-glacial origin were also found in the eastern part of the area.

Mawson’s activities in the Flinders Ranges during the 1920s were essentially of a reconnaissance nature and based on relatively little time, overall, spent in the field. The information included in the papers cited above demonstrate how much he could gain from a brief investigation, displaying his strength as a field worker and skill in rapidly appraising the geological situation in unknown country, and revealing his pre-eminence as an explorer-geologist. Work carried out during this period, while not yet part of a coordinated research programme, provided the basis for his later systematic approach to regional studies in the 1930s and 1940s.

Away from his empirical work in the field, he demonstrated a comparable ability to synthesise existing knowledge in a lengthy treatment of the igneous rocks of South Australia, delivered as a Presidential Address at the AAAS meeting at Perth in August 1926 (Mawson 1926b). This was an important review, given the widespread distribution and importance of igneous rocks,

notably in the older terrains of the State, but also in those of younger age. By discussing them region-by-region in their structural and stratigraphic context, he produced what was essentially a geology of the State. One issue of particular interest, not to be resolved for many years, was the age of the highly metamorphosed sediments on the eastern flank of the Mount Lofty Ranges and their associated intrusives. With reference to Howchin’s view that these rocks were the equivalents of the Adelaide Series, Mawson urged caution, pointing out: ‘the geological mapping of the Ranges is yet only in the early stages (and) final conclusions are unsafe until more detailed petrology and complete geological mapping have been accomplished’. As for the Victor Harbor granites Mawson comments perceptively: ‘there is yet no convincing evidence against the assumption of an early Palaeozoic age for this granite’.

Central Australia 1927

In November 1927, Mawson and Madigan made a short visit to Alice Springs and the Western McDonnell Ranges to check a mineral occurrence which had excited local interest. A white crystalline substance, long known to the aborigines and which burned with a fierce flame, was thought possibly to have some connection with petroleum. Specimens had been brought to Adelaide (initially to Madigan), and identified by Mawson as potassium nitrate (saltpetre or nitre) a rare mineral with some economic use in the chemical and explosives industries. Realising the opportunity for geological exploration in an area still little known geologically, Mawson quickly organised an expedition to investigate. They travelled north by train to Alice Springs, and their car journey out through the western ranges from Alice Springs blazed a trail through country never traversed by vehicle before. The deposit proved to be of organic origin, the long-time accumulation of animal droppings, of scientific but not economic interest.

Much of the route west ran along the strike of the well-exposed sedimentary beds which gave a general indication of the southward dipping succession between the Precambrian crystalline basement and known Ordovician rocks of the Horn Valley. Traverses were run and rough sections made at several localities along the way, including Ellery Creek, and over 10 000 feet of strata were measured. In the lower beds

'cryptozoal limestones' and organic structures similar to those from the Flinders Ranges were prominent in several areas, while worm tracks and traces of mollusc shells together with algal limestones distinct from those lower in the sequence were found in the younger beds. On the basis of his limited field evidence, the sedimentary sequence was divided into two divisions—the Pataknurra and Pataoorta Series, once again showing his flair for the rapid assessment of the general geological situation in a new area. He made tentative and essentially correct correlations between the central Australian rocks and the older sequences in South Australia. This first and, as it proved, only venture into central Australian geology was a major contribution to knowledge of the region, building on and revising the earlier work of Tate and Watt (on the Horn Expedition), H. Y. L. Brown, C. Chcwings and L. K. Ward.

Mawson visited London the following year where he exhibited photographs and specimens at the Geological Society. The results of the expedition were published by the Society (Mawson & Madigan 1930). While circumstances determined that Mawson never returned to the Centre, it seems likely that he always envisaged following up the promising results of his first trip. Madigan, meanwhile, had been captivated by the Centre and immediately began his own independent and wide-ranging researches into the geology of the region which were to produce some of his best work. This perceived 'take-over' by Madigan was resented by Mawson and led to bad feeling between the two men, but Mawson was soon to be occupied with other matters.

BANZARE 1929–31

Mawson was very much involved with Antarctic matters from 1929 through into the early thirties. BANZARE (The British, Australian and New Zealand Antarctic Research Expedition) differed from Mawson's previous expeditions in being ship-based. The program was carried out on two summer cruises (1929–30, 1930–31) and while no land bases were established, limited sorties were made ashore, notably on some of the sub-Antarctic islands. With the emphasis on marine science, much of the data was collected by systematically sounding the depth of the offshore waters, sampling the water column and dredging the bottom for biological specimens. Because of the nature of the expedition, geological work was restricted, although sediments collected from the

sea-floor adjacent to the land and the variety of ice-transported boulders dropped there provided abundant evidence of sedimentation and sedimentary processes in a modern glacial environment. The BANZARE expedition further inspired Mawson to continue his study of the ancient glacial deposits in the Flinders Ranges, and he was to do this with renewed vigour in the years ahead.

The extended geographical and geological knowledge of Antarctica resulting from the BANZARE voyages enabled Mawson to be the first to postulate the existence of an extensive landmass lying beneath the southern ice-cap and bounded by a wide continental shelf. Much of the evidence for the geological make-up of this buried continent came from the ocean-floor studies where dredged boulders proved to be rocks of continental type. Mawson envisaged that the mineral resources of Antarctica, the existence of which his expeditions had suggested but were yet to be proven, would be developed at some time in the future, and that underground mining operations could be carried out successfully despite the problems of climate and terrain.

End of an Era

Professor Edgeworth David died in 1934. In his later years he had become increasingly obsessed with his recognition of 'fossils' in the Precambrian rocks of South Australia (David 1928). Most of his finds had been made on visits to Adelaide at times when Mawson was away overseas or otherwise engaged on Antarctic business and had no chance to control these incursions. For Mawson it was particularly galling for David to hint that his old student was sitting on a rich treasure trove of Precambrian fossils while he, David, made the pickings, even enlisting Mawson's students and staff to help him collect. Wisely, Mawson held his counsel and endeavoured not to be drawn into the matter. It soon became clear, to almost all but David, that the supposed 'fossils' were in fact inorganic in origin (a verdict upheld by later workers), but he was to persist in his belief through to the end of his life, considering his discoveries in South Australia to be the highpoint of his career.

Deciphering the Flinders

In the mid-1930s Mawson renewed his long-

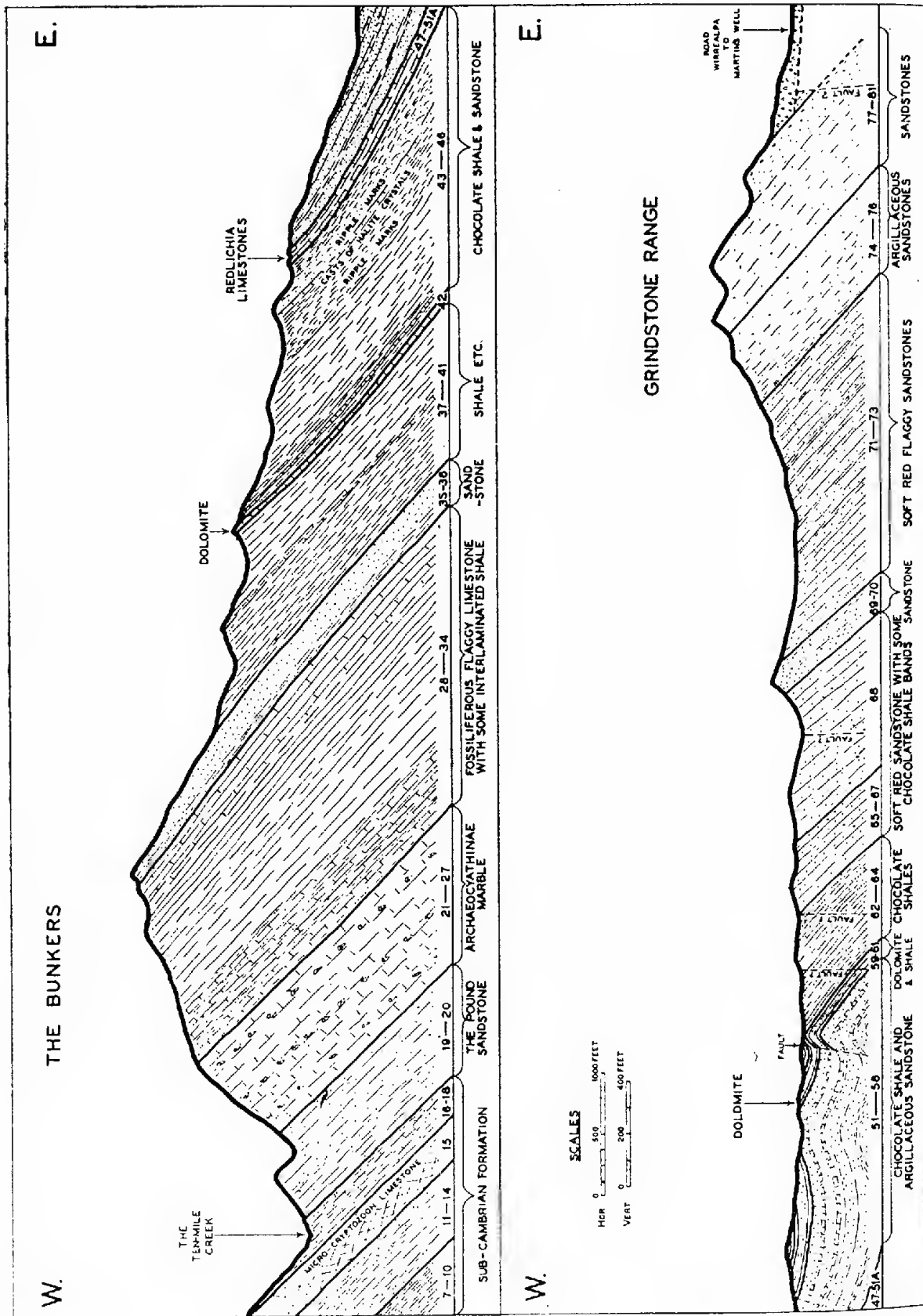


FIGURE 11. Stratigraphic section through the Bunkers and Grindstone Ranges. Mawson, 1939, fig. 2. Courtesy Royal Society of South Australia.

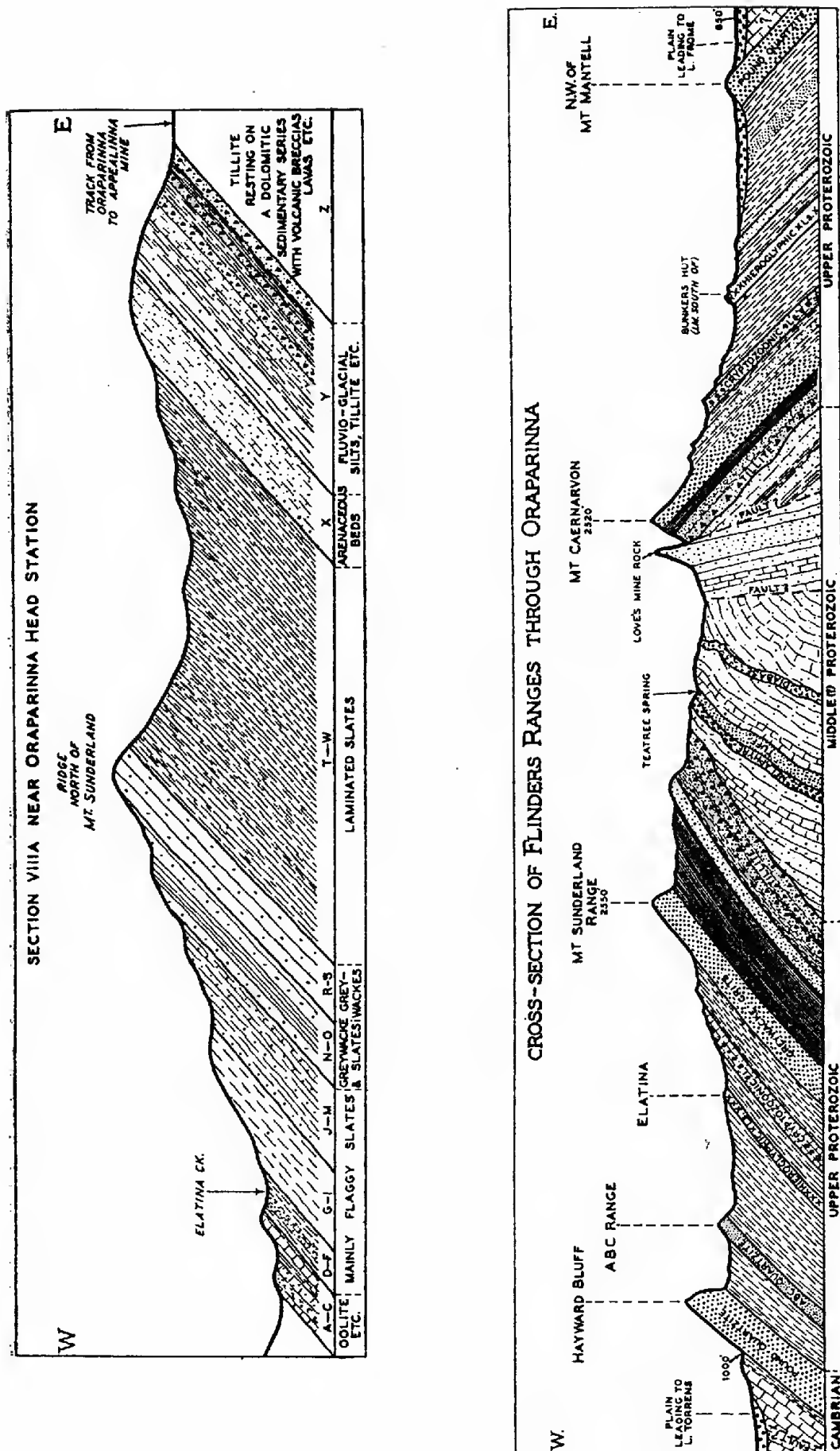


FIGURE 12. Stratigraphic sections near Oraparinna, Flinders Ranges. Mawson, 1942. Courtesy Royal Society of South Australia.

standing but formerly sporadic association with the Flinders Ranges. Now for the first time with fewer distractions, he was able to develop and pursue a sustained and systematic fieldwork program the results of which constitute his most notable contribution to South Australian geology. Only a brief resume of this work is given here, to be treated more fully in a later paper.

The Flinders Ranges were sparsely populated in the 1930s, and moving around in the outback more arduous than today. Roads and tracks were in general poorly maintained and motor transport, then in its infancy, was still an adventurous undertaking. There were no photo-based maps or accurate large-scale topographic maps available in those days, the only maps available being pastoral plans which were quite inadequate as a base for geological mapping. Mawson's approach was to select key sections which were measured and described in detail. In a few of his papers, small-scale regional maps were included. He first used aerial photography as an adjunct to his fieldwork in the late 1940s. Field-camps in the pre- and early war years combined the instruction of senior (third year) students in field techniques, including section measuring, with the gathering of basic geological information in country previously geologically unknown.

By 1939, having spent time in the Wooltana, Mount Carnarvon, Parachilna Gorge and Italowie areas, Mawson's work in the Flinders had reached a stage where review was warranted, and two publications in that year, on the Late Precambrian, and Cambrian successions respectively (Mawson 1939a, 1939b), detail rock sequences in the Brachina Creek-Oraparinna and Wirrealpa Basin areas of the central ranges (Fig. 11). The Pound Quartzite, the dominant ridge-former of the Flinders which occurs some distance stratigraphically below the oldest fossiliferous Cambrian rocks, was provisionally placed at the base of the Cambrian on lithological grounds and interpreted as marking the start of a new cycle of sedimentation. Defining the Precambrian-Cambrian boundary was to become of increasing interest to geologists in the years ahead, a task made no easier by the lack of fossils and by the absence of major breaks in sedimentation in the thick Upper Precambrian to Cambrian sedimentary sequence in South Australia. In his Wirrealpa Basin paper, two important fossiliferous units are described: the *Archaeocyatha Limestone* and a younger limestone (the *Wirrealpa Limestone*) first described by Howchin but here fully documented

for the first time with its fossil fauna of algal remains (*Girvanella*), brachiopods (*Obolella*), pteropods and trilobite fragments (*Redlichia*).

Other papers were to follow dealing with sequences in the Aroona, Copley, Brachina and Wilpena areas and culminating in an important review, 'The structural character of the Flinders Ranges' (Mawson 1942), which brought together the results of his fieldwork program to that time. A small scale map (Fig 13) showed the location of the key sections measured and the distribution of the rocks spanning the four main periods of deposition: the Middle Proterozoic and Late Proterozoic, the Cambrian and the Tertiary-Recent. Key marker beds, including the prominent Pound and ABC Quartzites, tillites and hieroglyphic limestones were also delineated. A cross-section (Fig. 12) indicated the essentially simple anticlinal structure of the central ranges. A wider-ranging paper (Mawson 1947) extended and amplified his earlier work, adding new information from the western flank of the ranges both in the north (near Copley) and in Mundallio Creek to the south. In both areas Mawson recognised thick quartzite formations at the base of the sequence, pointing out the error made by Segnit (1939), working for the Mines Department, who had equated these ABC Quartzite sequences with the Pound Quartzite. Mawson, however, was himself misled in the area west of Quorn where he mistook the prominent folded ABC Quartzite as Pound Quartzite (here thinly developed). Such are the dangers of making correlations on lithological grounds in rocks without fossils to act as age indicators.

Mawson also discussed the Flinders succession in its broader tectonic framework which he considered a major trough of deposition of Late Precambrian to Cambrian age and referred to as the 'great synclinal basin' (later to be named the Adelaide Geosyncline). His work had demonstrated the great thickness of strata deposited in the trough which extended south from Central Australia to the Adelaide region and lay between two ancient Precambrian massifs: Yilgarnia to the west and Willyamia to the east. The flat-lying sedimentary cover-rocks to the west of Port Augusta, believed on lithological and structural grounds to be correlates of the basal quartzites in the western ranges are now known to be ABC Range Quartzite equivalents. Wider correlations of the Flinders Ranges succession with the rocks of the western Mount Lofty Ranges (comparisons with the still largely unresolved sequence on the eastern flank of the Mount Lofty

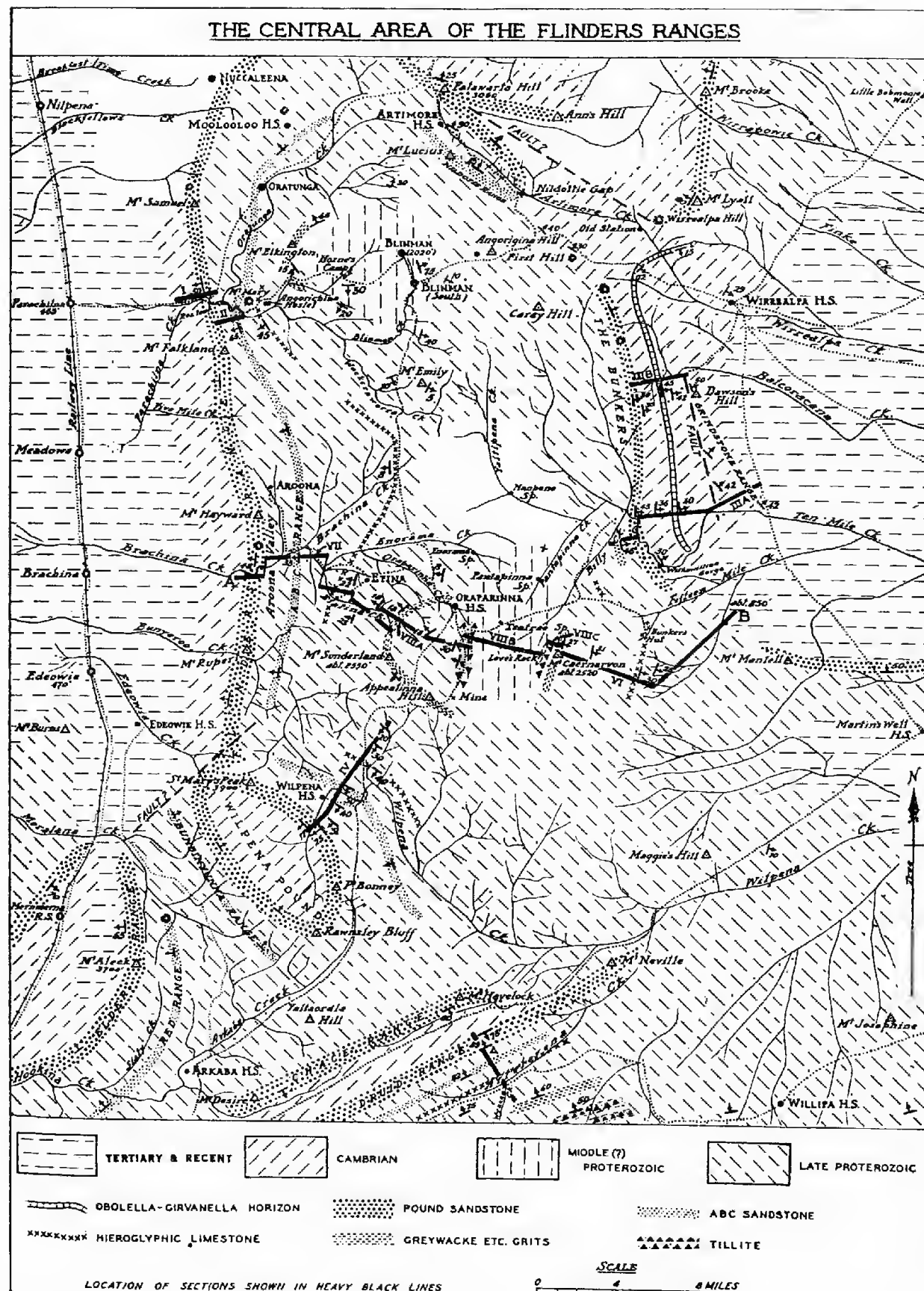


FIGURE 13. Mawson's geological map of the central Flinders Ranges. Mawson, 1942. Courtesy Royal Society of South Australia.

Ranges still remain highly speculative), with Central and Western Australia and also with South Africa (Transvaal System) were also suggested and discussed (Mawson 1947).

In the early 1940s Mawson returned to the North Flinders investigating the metamorphic effects of plug-like granite intrusions in the Precambrian country rocks (Mawson & Dallwitz 1945a,b). This study of both the sedimentary and igneous aspects of the geology of the region linked his early work on the older mineralised terrains in the Mount Painter area with his later concentration on unravelling the stratigraphy of the overlying sedimentary sequence.

Ancient Glaciation

Mawson first encountered evidence of ancient glaciation on his trip to the north Flinders in 1910. Subsequently he had demonstrated the widespread distribution of glacial rocks in the ranges during

his extensive field investigations (Fig. 14). His Antarctic experience of a glaciation-in-being, with the diversity of its products and processes, from the coarse boulder beds of terminal moraines to the finely layered sediments laid down in tranquil glacial lakes, had equipped him, as he had intended it should, to recognise the varied and not always easily interpreted evidences for former ice-ages.

By the late 1940s, Mawson had established the stratigraphic position of the Sturt Tillite in many areas of the Flinders and also identified a younger glacial episode in the Elatina area on the western flank of the central ranges (Mawson 1949a). The distinctive sediments—coarse sandy beds overlain by a thick unstratified boulder bed—first encountered in 1938, had initially been thought to be of pyroclastic origin (Mawson 1938) because of the preponderance of igneous pebbles in the rock.

Mawson then produced evidence for a third glacial event, this time predating the Sturt Tillite (Mawson 1949b), in the deeply eroded high



FIGURE 14. A large striated erratic weathered out of Proterozoic tillite, Yankaninna Station. Photo R. H. Jones. Mawson, 1945, pl. 14. Courtesy Royal Society of South Australia.

country of the Bibliando Dome east of Hawker. Here a thick sequence of glacials and associated beds revealed two extended periods of glaciation separated by a well-defined inter-glacial interval. The younger glacial event was equated with the Sturt Tillite while the older (lower) tillites were referred to as the Bibliando stage.

The clear demonstration of a third glacial phase in the history of the geosynclinal basin, with a broad range of deposits from boulder tillites through coarse fluvio-glacial sediments to fine laminated shales, raised such questions as the interpretation of past geographies, climates and environments, and the cyclic nature and causes of glaciation. Mawson, with his deep and extensive knowledge of ice-action both ancient and modern, was, more than any other geologist of his generation, aware of the diversity, complexity and the problems associated with interpreting glacial evidence. He discussed some of these in his paper on Bibliando, which marks the culmination of his career-long investigation of glacial phenomena. He took the opportunity to view this latest work in a broad historical perspective. The early discoveries of Selwyn, Tate and Howchin had placed South Australia at the forefront of research in the study and understanding of past glaciations. His own work had extended and clarified that knowledge, setting it within the wider context of the development of a major Upper Precambrian geosyncline, the importance of which had now become apparent.

While the rocks in the Flinders are magnificently displayed and accessible for study, the lack of fossils in the ancient rocks have always made the task of the stratigrapher difficult. Mawson, the first geologist to systematically approach the task of establishing an ordered succession was acutely aware of this problem. As his work proceeded and became recognised beyond South Australia, he perceived the need for a standardisation of geological nomenclature, particularly of stratigraphic names, and he was a member of the first committee set up by ANZAAS in 1947 which led to a Code of Stratigraphic Nomenclature being formalised in 1950.

Mawson favoured dropping the long-established but restricted Adelaide Series of David and Howchin and replacing it with the Adelaide System which he sub-divided into the Torrensian, Sturtian and Marinoan Series (Mawson & Sprigg 1950). The defining of the Adelaide System marked the end of Mawson's work on the old rocks of South Australia. The discovery of jellyfish fossils by Reg Sprigg in the

Pound Quartzite at Ediacara in 1946 (Sprigg, 1947, 1949), and the later finds of a diversified animal fauna by Flounders and Mincham, led to a reappraisal of the stratigraphy of the fossil-bearing beds (Glaessner & Daily 1959). Relegation of the Pound Quartzite from the base of the Cambrian (as previously suggested by Mawson) to the uppermost formation in the Precambrian meant that the Ediacara fossils, now confirmed as the oldest animals known, became world famous.

The South-East

Contrasting strongly with the rugged grandeur of the Flinders Ranges, the geologically youthful and topographically unchallenging south-eastern region of South Australia attracted Mawson from the mid-1930s. He became interested in the problematic 'coorongite', a rubbery bituminous substance first discovered in 1852 at Alf Flat east of Salt Creek at the southern end of the Coorong Lagoon (Fig. 15). A belief that the flammable material might be a petroleum product led to speculation that oil existed at depth; and several (unsuccessful) drilling attempts were made in the 1880s and again in the 1920s. By then almost all investigators had become convinced of the vegetable origin of the substance (and it has since been shown to be the product of algal blooms). Mawson, however, was unconvinced; and he inadvertently attracted overseas interest for a brief period when he took a visiting petroleum expert from Britain (Washington Gray) into the field to view the material and Gray went home to publicise the find, much to Mawson's chagrin. Some biochemical work was carried out overseas on the 'algal gel', but the matter was not pursued any further.

More substantial and fruitful work in the region led to a series of publications on the small and isolated outcrops of granitic rock which protrude through the thin Quaternary cover of the Upper Southeast. Fieldwork involved exploration on a minor scale, for many of the outcrops lay in difficult country accessible only on foot or horseback and where the outcrops were not extensive. The studies were carried out in association with students or former students and covered a quadrilateral bounded by Meningie and Coonalpyn on the north and Kingston and Bordertown to the south. The field investigations and subsequent analytical work led Mawson to recognise a variety of intrusive and extrusive rock



FIGURE 15. Mawson, with auger, drilling for coorongite, the Coorong, mid-1930s. Washington Gray on right. Source unknown.

types in the outcropping basement: granites; adamellites and granodiorites; and quartz keratophyres (volcanic). Similarities between the intrusives of the South-East and those occurring along the eastern flank of the Mount Lofty Ranges and on Kangaroo Island supported the concept of a large granitic batholith existing beneath the sedimentary cover, and, on the available evidence, Middle to Late Cambrian in age.

Finale

Mawson was sixty-three at the end of the Second World War and approaching the normal age for retirement. He continued on, however, to the age of seventy and spent his last university years rounding off his own researches and ensuring that his department was left in a healthy and secure position to meet the challenges ahead.

THE MAWSON LABORATORIES
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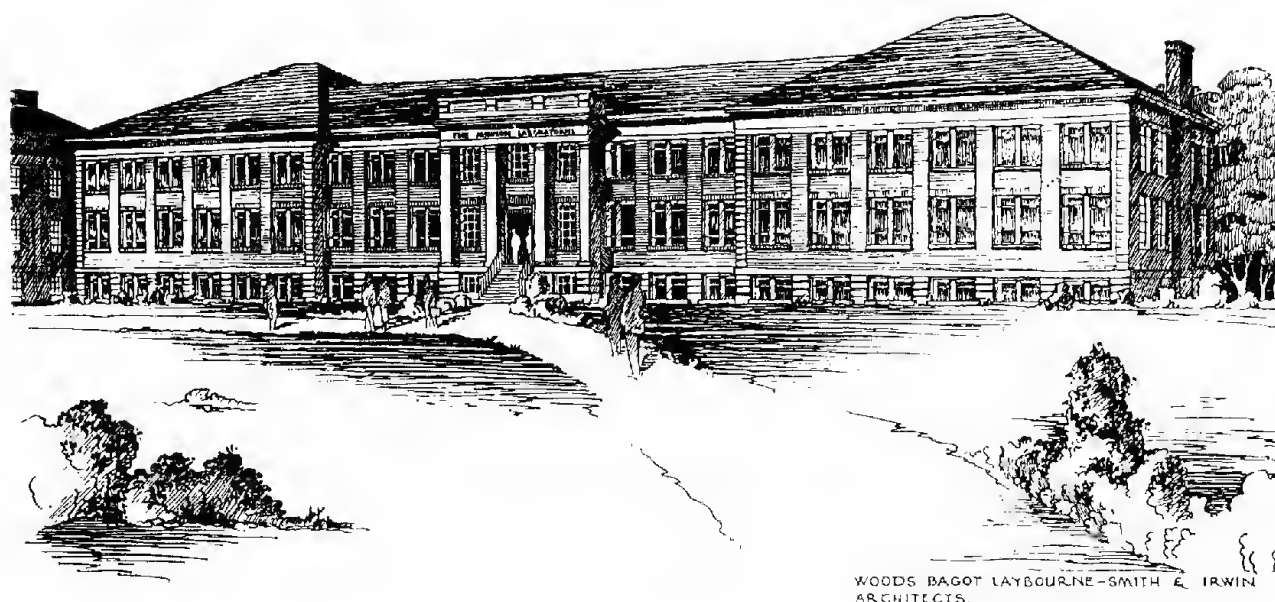


FIGURE 16. The proposed Mawson Laboratories. Courtesy Woods Bagot Pty Ltd, Adelaide.

He had been acutely aware of the greatly increased role that geology would be required to play in the post-war world. In particular, well trained geologists could only be supplied by the universities which in turn would need to provide a sufficient level of support in terms of accommodation, equipment and staffing. In all these areas Mawson had been struggling against inadequacies for over twenty years. During this time, geology had made the best of sub-standard accommodation and increasingly inadequate provision for research, whereas the rest of the University had developed and prospered. It was the urgent need for a better deal for geology that prompted his memorandum to the University authorities in February (1944a). In his memorandum Mawson wrote: 'The department suffers from insufficiency of room, from inadequacy of the laboratories, and from the entire absence of any planned layout suitable for a science department. All other science departments of the University now have buildings specially planned for their needs though some are already proving too limited in accommodation for the flood of students now presenting themselves. Ours is an anachronism'.

He went on to make a very strong case for the role of geology in education, its application to

national development and significantly, South Australia's importance as a source of future mineral resources. He envisaged Adelaide University as a future centre for teaching and research in economic and mining geology and itemised the basic needs of a modern School of Geological Studies, estimating the cost of the new development at around £25 000.

His argument was decisive. The University responded appropriately, if belatedly, and the Mawson Laboratories were constructed, largely to his specifications, between 1949 and 1952 (Fig. 16). He just had time to move into the new building before retirement. By then his staff had increased to five and included E. A. Rudd who was appointed to the new Chair of Economic Geology in 1949, and Martin Glaessner, a palaeontologist with an international reputation who was to become the authority on the Precambrian fossils from Ediacara. Arthur Alderman, former student and junior lecturer in the department, returned after a period away from the University to take over from Mawson as Professor of Geology and Mineralogy in 1953.

In the years following his retirement Mawson remained active and influential in Antarctic matters and continued his long association with the South Australian Museum as Honorary

Curator of Minerals and Member of the Museum Board. He was appointed Chairman of the Board in 1952.

Douglas Mawson's broad interests in all aspects of geological science and his unfailing encouragement and support of young people with an enquiring mind and an interest in science is well illustrated by the background to his last published paper (Mawson 1958). It deals with australites (small glassy objects of meteoritic origin) collected by a young schoolboy, Mervyn Pens, from the Murray Plains west of Morgan in the mid-1930s. Mawson had visited the site and established a correspondence with young Pens, which led to further finds and ultimately to the public acquisition of a large and significant collection of australites now housed in the South Australian Museum. The paper was read before the Royal Society of South Australia on 10 October 1957. Sir Douglas Mawson died on 14 October 1958.

Mawson's Legacy

Mawson's inborn qualities as an explorer, his methodical approach to the job in hand, his tenacity and resolution and an ability to inspire and motivate others were revealed as much in his career as an academic geologist as in his exploits as an Antarctic explorer. He was essentially a man of action, a trail-blazer, single-minded in the pursuit of his goals, at times impatient for results, and who could, at times, be protective to the point of touchiness, of his own areas of interest. His inherited characteristics, hard-headed Yorkshire practicality, stubbornness and reticence, with a streak of romanticism (from his father) were blended with a pioneer Australian belief in opportunity and self-reliance to produce a complex character of contrasting and at times conflicting elements. He was a man not easily assessed or categorised. Geology is arguably the most adventurous of all the field sciences (the first scientist to visit the moon was a geologist), and Mawson in his life and career, both in the Antarctic and in his geological investigations in outback South Australia, exemplified both the scientific-explorer and explorer-scientist.

Mawson's scientific career spanned, almost exactly, the first half of the twentieth century. When he entered the University of Sydney in 1899 the scientific world-view was of a cooling, shrinking earth not more than one hundred million years old, the limits having been set by the

physicists. Geologists, whose investigations had by then spread to all parts of the globe, intuitively sensed a more ancient earth but lacked the means to prove it. Mountain belts were seen as a crustal adjustment to a cooling interior and most geologists accepted the relative permanence of the continents and oceans.

In retrospect, the years 1900–1950 can be viewed as a relatively quiet episode in the development of geological science, enlivened by two developments early in the century: the application of the discovery of radioactivity to the dating of rocks, and Wegener's hypothesis of continental drift. Each in its own time, the first rapidly, the second much more slowly, became a vital element in the future Plate Tectonic revolution. The recognition that the decay of radioactive minerals produced heat freed geologists from the shackles of a cooling earth and a restricted time-scale by providing a source of self-sustaining energy and a means of dating the crustal rocks. By 1914, the estimated age of the earth had been pushed back to over one thousand million years. Mawson's work on radioactive minerals in Australia as a young student and his later discoveries in South Australia gave him a pioneer role in this new development and he was always very proud of his work in this field (see Mawson 1944b). But in his day Australia was effectively too remote from the rest of the world for its small and largely inaccessible deposits to be economically viable, and its universities (certainly Adelaide) too poor to engage in expensive age-dating equipment. In his later years Mawson was keenly interested in these developments overseas and their future potential for dating the old rocks in Australia.

Communication between scientists was severely curtailed during the two world wars which dominated the first half of the century, although technical developments during the second war were to help revolutionise geological and geophysical exploration both on land and in the ocean basins. Mawson's own career was savagely disrupted by the First World War and his more active years were over before the benefits of post-Second World War technical advances became widely felt. The inter-war years and those immediately after the second war were his most productive period for research, more particularly from the mid-1930s when his active involvement in Antarctic exploration had ended. Although the general outline of South Australian geology was well known by this time, no systematic work had been attempted and for much of the State

information remained highly generalised and lacking in detail. As previously indicated, Mawson's early researches were essentially exploratory reconnaissances, becoming more systematic with his work in the Flinders from the 1930s. His detailed descriptions of rock units and measured cross-sections of key sequences provided the basis for the regional mapping program to be instigated by the Geological Survey in the 1960s.

Mawson's research was very much an integral part of the growth and development of his department. His field studies in the Flinders were carried out with small groups of advanced students as part of their course work, while in the Southeast he published in collaboration with post-graduate and former students as well as directing them in projects of their own. His teaching is remembered by past students as being of variable quality; he was at his best, according to Alderman, when extemporising on subjects that particularly interested him. There is no doubt that he could inspire his students and a considerable number went on to make distinguished careers in geology and mineralogy, among them E. A. Rudd, L. W. Parkin, R. C. Sprigg, W. B. Dallwitz, D. E. Thomas, E. R. Segnit, B. Skinner, R. L. Crocker, M. Reynolds, B. Daily, R. Sweatman, A. Kleeman, B. Forbes and G. Chinner.

Mawson, the man of action, always seemed to have been fighting a lack of time to complete his projects; always planning another field trip and, one senses, chafing at the administrative burden placed on him as a highly responsible and consistently conscientious head of department. Never an armchair geologist, Mawson did not have the time or the inclination to become involved with the theoretical issues of the day, the most contentious of which was the idea of continental drift. Sir Mark Oliphant, a science student at the University in the 1920s, has recalled attending a debate on the subject between Mawson and Wood-Jones the anatomist, during which Mawson scathingly dismissed the concept of drift, citing the rigidity of the ocean floors and the lack of any known mechanism that could power the process.

Sir Douglas Mawson made an outstanding contribution to South Australian geology. His list of 102 publications, the majority published in the *Transactions of the Royal Society of South Australia*, provide the material evidence of his work. He also left a strong department which he had established and which was developing rapidly in teaching and research. While it is idle to speculate, one cannot help but wonder what he might have accomplished as a geologist if so much of his time and energy had not been devoted to the Antarctic. He was not able to settle down to an ordered academic life and an on-going research program until he reached his fifties. From then on his geological output was sustained until the end of his career. It was a remarkable achievement.

ACKNOWLEDGMENTS

The research on which this paper is based was begun when the author was a staff member in the Mawson Graduate Centre for Environmental Studies at the University of Adelaide and completed as an Honorary Research Associate at the South Australian Museum. It relies heavily on a study of the Mawson Papers housed in the Special Collections archive of the Barr Smith Library, The University of Adelaide, and Mawson's published papers. Research was also carried out on the Edgeworth David papers held by the Fisher Library at the University of Sydney and in the library of the Scott Polar Research Institute, Cambridge.

For valuable assistance during the course of this work, thanks are due to: Susan Woodhurn and the staff of Special Collections, The University of Adelaide; Mr Ken Smith, Archivist, The Fisher Library and Professor David Branagan, The University of Sydney; Mr Robert Headland, Curator and Archivist, The Scott Polar Research Institute, Cambridge.

For on-going encouragement and support for this research and for much helpful discussion on matters relating to Mawson, grateful thanks are extended to Mr Richard Ferguson, Polar historian; Emeritus Professor E. A. Rudd, The University of Adelaide; Dr Victor Gostin of the Geology Department, The University of Adelaide and Dr Allan Pring, Curator of Minerals, The South Australian Museum. Particular thanks are due to Dr Robin Oliver of the Geology Department, University of Adelaide, for his critical review of the original draft of this paper, and his many useful suggestions.

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REVISION OF AUSTRALIAN *ENOCHRUS* THOMSON (COLEOPTERA: HYDROPHILIDAE)

C. H. S. WATTS

Summary

The Australian members of the hydrophilid genus *Enochrus* are revised and redescribed. A key to the fourteen species recognised is given. Six species are described as new: *E. aliciae*, *E. eubenangeei*, *E. isabellae*, *E. pseudoweiri*, *E. samae*, and *E. weiri*. The following synonymies are proposed: *E. mjobergi* Knisch, 1921 = *E. deserticola* (Blackburn, 1896); *E. andersoni* (Blackburn, 1896) = *E. eyrensis* (Blackburn, 1894); *E. persimilis* Regimbart, 1908 = *E. eyrensis* (Blackburn, 1894); *E. pullus* (Fauvel, 1883) = *E. esuriens* (Walker, 1858) and *E. artensis* (Fauvel, 1883) = *E. maculiceps* (MacLeay, 1873). The New Caledonian species *E. caledonicus* (Fauvel, 1883) is considered a synonym of *E. elongatus* (MacLeay, 1873).

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WATTS, C. H. S. 1998. Revision of Australian *Enochrus* Thomson (Coleoptera: Hydrophilidae). *Records of the South Australian Museum* 30(2): 137–156.

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Manuscript received 19 March 1997.

The hydrophilid genus *Enochrus* Thomson, 1859 is world wide in distribution (Hansen 1991). In Australia its members are the commonest and most widespread hydrophilids and occur in virtually all fresh water bodies from small stagnant pools to the banks of major rivers and lakes. Despite this prominence, their taxonomy is so bad that no species can be identified with any confidence. Thirteen species have been named and several others have been recorded as being present but until now no revision has been attempted.

Australian *Enochrus* are structurally very similar and difficult to separate. Apart from the aedeagi the only characters that I have found useful are size, the punctuation of the upper surface, the slope of the mesosternal keel, and the colour pattern of the head. The colour pattern of the head is often a reasonable indicator of species, whereas elytral and pronotal colour can vary from predominantly black to totally light reddish in the same species.

Within *Enochrus* six subgenera are recognised (Hansen 1990). Three of these occur in Australia: *Hydatotrephis* MacLeay, 1873 with one species; *Enochrus* Thomson, 1859 with one species; and *Methydrus* Rey, 1885 with 12 species.

At first sight *E. (H.) mastersi* is very similar to the distantly related *Limnoxenus zealandicus* Broun and is often confused with it in collections. Both are moderate sized (10–15 mm), shiny black and relatively common, particularly *L. zealandicus*. A closer inspection readily separates them: *L. zealandicus* has well defined punctate elytral striae and swimming hairs on the meso-

and meta-tibiae, both of which are absent in *E. (H.) mastersi*. Characters of the maxillary palpi and mesosternum also separate the two genera (Hansen 1990).

The one Australian *Enochrus* (*Enochrus*) species, *E. (E.) peregrinus* Knisch, 1922, is small and in general appearance resembles several Australian *Enochrus* (*Methydrus*) species. It is known from only one specimen labelled from Sydney, although there were three in the original collection. It may eventually prove to have been mis-labelled and not Australian.

The remaining 12 Australian species are all in the subgenus *Methydrus*. They are usually small (2–8 mm), oval, rather flat species, shiny with light-testaceous to black colouring with at least the area immediately in front of the eyes yellowish. Two species are larger and predominantly black, superficially resembling *E. (H.) mastersi*. *Chasmogenus nitescens* Fauvel resembles some *Enochrus* (*Methydrus*) species and is often confused with it in collections. Its small size (< 5 mm) and lack of yellowish areas in front of its eyes readily separate it from similar sized *Enochrus* – as well as many structural characters mentioned later under 'Systematics'.

One additional species, *Philhydrus marmoratus* W. MacLeay, 1873, has been included in *Enochrus* in the past but has been shown by Gentili, 1981 to belong in *Laccobius*.

For a full discussion of synonyms and subgenera of *Enochrus* see Hansen, 1991.

Despite their being ubiquitous in freshwater the biology of Australian *Enochrus* is poorly known.

Anderson (1976) described the larvae of *E. (M.) maculiceps* and *E. (M.) elongatus* and gave brief notes on their habitat and breeding. All species come readily to light and are often collected in large numbers in light traps, particularly in northern areas during the wet season from December to February. I know of no study of the ecology of any Australian species other than inclusion in general faunal lists of invertebrates collected in various water bodies.

The collections from which specimens were examined are listed under the following abbreviations:

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection
BM(NH)	Natural History Museum, London
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
MNHN	Muséum National d'Histoire Naturelle, Paris
NMV	Museum of Victoria
NRS	Naturhistoriska Riksmuseet, Stockholm
NTM	Northern Territory Museum
QDPIM	Queensland Department of Primary Industries, Mareeba
QM	Queensland Museum, Brisbane
SAMA	South Australian Museum, Adelaide
UQIC	University of Queensland Insect Collection, Brisbane
WAM	Western Australian Museum, Perth.

SYSTEMATICS

Australian members of the genus *Enochrus* can be separated from other Australian Hydrophilids by the following combination of characters. Length 2–9 mm, oval, more flattened than convex; second segment of maxillary palpi more or less curved outwards, apical segment slightly asymmetrical with straighter inner face; without contiguous ventral keel but with variable keel on mesosternum; without swimming hairs on tibiae; without strongly marked striae on elytron; with systematic punctures (rows or fields of coarse setiferous punctures usually distinctly larger than others) on head and pronotum (masked in some *E. malabarensis*); in all but *E. mastersi* and *E. aliciae* at least the area immediately in front of eyes lighter (see also Hansen 1991).

The subgenus *Hydatotrepis* MacLeay can be

separated from Australian members of the subgenera *Enochrus* Thomson and *Methydrus* Rey as follows: mesosternal protuberance triangular, cone-shaped, abruptly truncated posteriorly which does not reach the front edge of mesocoxae (Fig. 19), sides of mesosternum evenly converging anteriorly, apical and penultimate segments of maxillary palpi subequal. *Enochrus (Methydrus)* have a more keel-like mesosternal process usually extending backwards between the mesocoxae (Figs 15–18; 20), the apical segment of the maxillary palpi shorter than penultimate and sides of mesosternum subparallel to strongly convex anteriorly. Apart from *E. (M.) aliciae* and *E. (M.) eubenangeei*, the Australian members of *E. (Methydrus)* are smaller (< 8 mm), often testaceous in colour, and have at least a lighter patch of colour in front of the eyes.

The aedeagus of *E. (H.) mastersi* differs from that of other Australian *Enochrus* (Fig. 14; Hansen 1990). In these there is a variably shaped basal ventral plate beyond which projects a thinner apical portion in all but *E. (M.) aliciae* which lacks this apical portion (Fig. 11). In *E. (H.) mastersi* the aedeagus is of more uniform construction with a smooth dorsal surface and the ventral surface consists of a broad open groove formed by infolding of the two sides.

There is one species, *E. (E.) peregrinus* Knisch, of the subgenus *Enochrus* in Australia. It is similar in looks to the smaller *Methydrus* species but is readily separated from them by the short stout maxillary palpi with approximately equal sized apical two segments and the diverging elytral suture lines.

By utilising the male genitalia species can be differentiated. However without these I have found it impossible to reliably separate all species, in particular *E. weiri* and *E. pseudoweiri* and the lighter colour phase of *E. deserticola* and *E. maculipes*. This is reflected in the keys and descriptions that follow. I have restricted my descriptions to the few characters that serve to differentiate the species and I have provided two keys, one utilising all available characters, the other characters other than the male genitalia.

KEY TO AUSTRALIAN *ENOCHRUS* THOMSON 1859, NOT USING CHARACTERS OF THE MALE GENITALIA

1. — Maxillary palpi stout, first segment shorter than distance from front edge of eye to front of clypeus, apical segment subequal in length to penultimate 2
- Maxillary palpi more elongate, first segment

- longer than distance from front edge of eye to front margin of clypeus, apical segment about 2/3 length of penultimate (subgenus *Methydus*) 3
2. — > 6.0 mm. Black. Sutural lines on elytra subparallel in anterior quarter
 *E. (Hydatotrephis) mastersi* (MacLeay)
 — < 5.0 mm. Dark testaceous. Sutural lines on elytra diverging noticeably in anterior quarter ..
 *E. (Enochrus) peregrinus* Knisch
3. — Large (>6 mm). Black (pronotum may be reddish at edges) 4
 --- Small (< 6 mm). With at least the areas in front of eyes reddish-yellow 5
4. --- Punctures towards sides of elytra well impressed, not much smaller than others
 *E. (M.) eubenangeei* sp. nov.
 — Punctures towards sides of elytra subobsolete, much smaller than those on disc
 *E. (M.) aliciae* sp. nov.
5. — Dorsal surface reddish-yellow, rear of head at most somewhat darker. Elytra moderately punctate, length > 4.0 mm, pro-, meso- and metac claws modified in male.
 *E. (M.) elongatus* (W. MacLeay)
 --- Dorsal surface reddish-yellow to black, rear of head dark and much of rest of head in many species, males with only pro-claws modified 6
6. — Dorsal surface strongly punctured, punctures on elytra as strong or stronger than those on head, many punctures on elytra > half diameter of serial punctures which are often hard to trace. Front of head 1/3 or more black 7
 — Dorsal surface weakly punctured, punctures on elytra tend to be weaker than those on head, punctures on elytra < half size of serial punctures which are usually distinct 9
7. — Length > 3.5 mm. Black morphs present. Maxillary palpi with dark tips 8
 — Length < 4.0 mm. Black morphs not known. Maxillary palpi usually pale throughout
 *E. (E.) malabarensis* Régimbart
8. — Thinner outer portion of mesosternal keel well developed (Fig. 16). Front of head predominantly black
 *E. (M.) eyrensis* (Blackburn)
 — Thinner outer portion of mesosternal keel less developed (Fig. 15). Amount of black on front of head variable *E. (M.) samae* sp. nov.
9. — Length 2.2 mm – 2.6 mm. Mesosternal keel weakly developed (Fig. 18). Front of head > 2/3 black *E. (M.) esuriens* (Walker)
 — Length > 2.6 mm. Mesosternal keel well developed (Fig. 17) 10

10. — Larger (4.5–6 mm). Black, except region in front of eyes light. Elytral punctures small but usually well inarked
 *E. (M.) isabellae* sp. nov.
 — Smaller (3–4.5 mm) *E. (M.) deserticola* complex (*E. (M.) deserticola* (Blackburn), *E. (M.) maculiceps* (W. MacLeay), *E. (M.) weiri* sp. nov and *E. (M.) pseudoweiri* sp. nov). (*E. (M.) deserticola* only species with black morphs and individuals > 4.2 mm long. *Enochrus weiri* and *E. pseudoweiri* always have pale palpi.)

KEY TO AUSTRALIAN *ENOCHRUS* INCORPORATING CHARACTERS OF THE MALE GENITALIA

1. — Maxillary palpi stout, pseudo first segment shorter than distance from front edge of eye to front of clypeus, apical and penultimate segments subequal in length 2
 — Maxillary palpi more elongate, pseudo first segment longer than distance from front edge of eye to front margin of clypeus, apical segment noticeably shorter than penultimate (subgenus *Methydus*) 3
2. — > 6.0 mm. Black. Sutural lines on elytra subparallel in anterior quarter
 *E. (Hydatotrephis) mastersi* (MacLeay)
 .. < 5.0 mm. Dark testaceous. Sutural lines on elytra noticeably diverging in anterior quarter ..
 *E. (Enochrus) peregrinus* Knisch
3. — Large (> 6.0 mm). Black (pronotum may be reddish at edges) 4
 — Small (< 6.0 mm). With at least the areas in front of eyes reddish-yellow 5
4. — Aedeagus broad reaching little beyond half length of parameres (Fig. 11). Parameres flat.
 *E. (M.) aliciae* sp. nov.
 Aedeagus with broad basal piece and long thin apical piece bending upwards and reaching nearly to end of parameres, which also bend upwards (Fig. 10)
 *E. (M.) eubenangeei* sp. nov.
5. — Tips of parameres hooked (e.g. Fig. 4) 6
 — Tips of parameres not hooked (e.g. Fig. 1) 9
6. — Dorsal surface reddish-yellow, rear of head at most somewhat darker. Aedeagus tip strongly crotchet-shaped (Fig. 7). Pro-, meso- and metac claws modified in male
 *E. (M.) elongatus* (W. MacLeay)
 --- Variably coloured but always with rear of head clearly darker than at least portions of front of head. Aedeagus with little or no dorsal/ventral expansion at tip, males with only proclaws modified 7

7. — Dorsal surface strongly punctured, many punctures on elytra > half size of serial punctures *E. (M.) eyrensis* (Blackburn)
 - Dorsal surface weakly punctured, punctures on elytra < half size of serial punctures 8
8. — Larger (4.5–6.0 mm). Black, except in front of eyes. Aedeagus shorter and apical portion broader (Fig. 6) *E. (M.) isabellae* sp. nov.
 - Smaller (3.0–4.0 mm). Pale morphs common. Aedeagus longer and apical portion thinner (Fig. 4) *E. (M.) deserticola* (Blackburn)
9. — Length <2.8 mm. Front of head $\geq 2/3$ black. Mesosternal keel weak (Fig. 18) *E. (M.) esuriens* (Walker)
 - Not as above 10
10. — Dorsal surface strongly punctured, punctures on elytra as strong as, or stronger than, those on head, many punctures on elytra > half diameter of serial punctures 11
 - Dorsal surface weakly punctured, punctures on elytra tend to be weaker than those on head, punctures on elytra < half size of serial punctures 12
11. — Larger (4.4–5.6 mm). Black morphs present. Aedeagus with moderate apical pad, inner edges of parameres sinuate (Fig. 9) *E. (M.) samae* sp. nov.
 - Smaller (<3.8 mm). No black morphs. Aedeagus narrow with, at most, a weak pad, inner edges of parameres straight (Fig. 12) *E. (M.) malabarensis* Régimbart
12. — Tips of parameres truncated or weakly bifid (Fig. 8) *E. (M.) weiri* sp. nov.
 - Tips of parameres rounded (Figs 1, 2, 3) 13
13. — Aedeagus moderately broad with slight to well-marked apical pad (Figs 1, 2) *E. (M.) maculiceps* (W. MacLeay)
 - Aedeagus narrow, sharply pointed, lacking apical pad (Fig. 3) *E. (M.) pseudoweiri* sp. nov.

DESCRIPTIONS

Subgenus *Enochrus*

Enochrus (Enochrus) peregrinus Knisch, 1922

Types

Lectotype: ♀ 'Sidney Mus. Godeffroy No. 10705, coll. Knisch, coll. d'Orchymont'; 'ex. col. Knisch, No. 5251438, coll. d'Orchymont';

'Knisch det. 1921, *Enochrus peregrinus* m'; 'Coll. A. Knisch, TYPUS', on red card, in IRSNB, herein designated.

Knisch (1922) mentioned three specimens (No. 10705) in the Hamburg Zoological Museum. I have been able to trace only one. He mentioned that one was labelled 'M. Régimbart det. 1905' and the others with 'Wehncke determ'. The surviving specimen, now in Brussels, lacks such a label but would otherwise appear to be part of the syntype series.

Description (number examined, 1)

Length 3.2 mm. Broadly oval. Elytra dark-testaceous, pronotum very slightly lighter, head black except for small indistinct testaceous patch along margin in front of each eye, maxillary palpi light-testaceous, tips darker. Punctures on head moderate, approaching size of eye facet, most separated from each other by at least puncture width. Systematic punctures rather sparse, about twice diameter of adjacent punctures. Pronotum rather weakly and sparsely punctured, serial punctures also relatively small, indistinct, about 2x diameter of adjacent punctures, punctures on elytra stronger than on pronotum, sparse, many 2x diameter or more apart, a little stronger laterally. Serial punctures not traceable. Maxillary palpi short, stout, pseudo basal segment not reaching front edge of eye, apical and penultimate segment subequal in size.

Male: Unknown.

Distribution

Known only from Sydney, the type locality.

Remarks

This unique specimen is separated from all other Australian *Enochrus*, other than the much larger *E. mastersi*, by the short stout maxillary palpi. The masking of the elytral striae punctures is found only in the much larger *E. eyrensis* and *E. samae* and in *E. malabarensis*. *Enochrus malabarensis* differs from *E. peregrinus* by the more normal (for Australian species) maxillary palpi, the more extensive testaceous areas in front of the eyes and lighter coloured elytra. The elytral sutures continue to diverge noticeably in anterior quarter whereas in *E. malabarensis* they are subparallel. Most *E. malabarensis* also have stronger punctures, but this character is variable and tends to be relatively weak in the few Sydney area specimens I have seen. The pronotal punctures in *E. peregrinus* are weaker than those on elytra whereas in *E. malabarensis* they are similar sized.

The fact that only the type specimen is known worries me. For all the other small Australian *Enochrus*, specimens are relatively abundant. Also it is the only known specimen in the Australian region of the subgenus *Enochrus* (Hansen 1990). This is the sort of situation where mislabelling should be considered. This is beyond the scope of this revision.

Subgenus *Hydatotrephis*

Enochrus (Hydatotrephis) mastersi (MacLeay)

Hydatotrephis mastersi MacLeay, 1871

= *Farana simplex* Knisch, 1922: Hansen, 1990

Enochrus (Hydatotrephis) mastersi (MacLeay): Hansen, 1990

Types

Hydatotrephis mastersi: Lectotype: (♀), (round red label), 'K 19501', '*Hydatotrephis mastersi* Mc L.W. Gayndah'. 'Lectotype: *Hydatotrephis mastersi* W. J. MacLeay designated by M. Hansen 1990', AM.

Farana simplex: Lectotype: (unsexed) 'Sidney Mus. Godeffroy. No. 10704'; '*Philhydrus* x M. Régimbart determ. 1905'; '*Farana simplex* Knisch n.g. et sp. A. Knisch det. 1921', round black label; 'Lectotype *Farana simplex* Knisch designated by M. Hansen 1988', IRSNB. Synonymy after Hansen 1990.

Description (number examined, 71) Figs 14, 19

Size 8.0 mm – 9.1 mm. Broadly oval. Relatively flat. Black; lateral edges of elytra, pronotum and head, palpi and apical portions of legs diffusely dark-testaceous. Maxillary palpi stout, length about width of head in front of eyes, apical and penultimate segments subequal in length, together a little larger than pseudo first segment. Head strongly punctured, each about size of eye facet, most closer than a puncture width apart, systematic punctures 2–3x size of normal punctures. Pronotum with punctures a little smaller, shallower and more separated than on head, systematic punctures well marked, with sharp groove sometimes weak or lacking on front edge. Elytra punctured as on pronotum, each elytron with four rows of larger serial punctures, punctures in rows increasing in both number and scatter towards sides, elytra weakly grooved and flanged laterally, a few scattered large punctures between puncture rows two and three counting from suture. Mesosternal keel conc-like, strongly

raised, narrowly triangular from both lateral and front views, sharply truncated behind just prior to mesocoxal cavities so that no part of the keel extends between mesocoxae.

Male: Aedcagus broad, lacking collar or ventral plate, sides folded in ventrally tending to form broad channel. Parameres stout, broad, narrowing shortly before tips which tend to be turned inward to varying degrees.

Distribution

Australian Capital Territory

Black Mt, ANIC; Canberra, SAMA, ANIC; 3 km E Piccadilly Circus, ANIC; 6 km NE Piccadilly Circus, ANIC.

New South Wales

Allyn River, ANIC; Barrington River, ANIC; Blue Mts, ANIC Chichester St Forrester, ANIC; Coffs Harbour UQIC; Como, ANIC; Galston, SAMA; Lansdowne via Tarec, ANIC; Muswellbrook, ANIC; Nerringa, SAMA; 12 km NW Nellinger, ANIC; 2km NE by N Rousmill, ANIC; Salisbury UQIC; Stanwell Park UQIC; Sydney, SAMA, ANIC; Tooloom Plateau via Woodenbong UQIC; Ulladulla, ANIC; Valery, ANIC; Wee Jasper, ANIC.

Northern Territory

30 ml W Alice Springs, SAMA; Stanley Chasm, SAMA.

Queensland

Brisbane UQIC; Bulburin State Forest via Many Peaks UQIC; Bunya Mt, ANIC; Carnarvon UQIC; Discot, ANIC; 13 km SW by S Gordonvale, ANIC; Joalah Nt Pk Tamborine Mt, ANIC; Mt Norman, via Wallangarra UQIC; Mt Spec, ANIC; Upper Cedar Ck, via Sandford UQIC; 8 km E Wallaman Falls, SAMA.

Victoria

Bagots Ck, SAMA; Ferntree Gully UQIC; Healesville, SAMA; 10 mls N of Valencia Creek via Maffra UQIC; Victorian Alps, SAMA.

Remarks

A widespread and relatively common species which, within Australian *Enochrus*, can only be confused with *E. aliciae* and *E. eubenangeei*. It is readily separated from these species by the stout maxillary palpi which have the last two segments subequal instead of having the apical segment about two-thirds the length of the penultimate as

in all other Australian *Enochrus*. The cone-like shape of the mesosternal keel is also diagnostic.

Enochrus mastersi is most frequently confused with a very different, but similar looking and very common species, *Limnoxenus zealandicus*, of the subtribe Hydrobiina. Although very similar in general appearance *Limnoxenus* can be separated from *E. mastersi* by the presence of nine well-marked series of punctures on each elytron, swimming hairs on the meso- and metatarsi and virtual absence of rugose portions on meso- and metafemora.

Subgenus *Methydrus*

Enochrus (Methydrus) aliciae sp. nov.

Types

Holotype: ♂, '15°16'S, 144°59'E, 14 km W by N of Hope Vale Mission, Qld, 8–10 Oct. 1980, T. Weir', ANIC.

Paratypes: 13, same data as holotype, 10 ANIC, 3 SAMA; 1, '12°31'S, 132°54'E, 9 km N by E of Mudginbarry Hs., N.T., 10.vi.1973, T. Weir and A. Allwood, '13985', NTM.

Description (number examined, 17) Figs 11, 20

Length 7.5 mm – 8.2 mm. Broadly oval, relatively flat. Shiny, black, appendages, apical and lateral edges of head, pronotum and elytra dark-reddish. Maxillary palpi moderately long, pseudo first segment longer than distance from eye to front of clypeus, longer than maxillary stipe, apical segment $\frac{2}{3}$ to $\frac{3}{4}$ length of penultimate. Head strongly punctate, punctures about puncture width apart, about size of eye facet or a little smaller. Systematic punctures large about 3x size of adjacent punctures. Punctures on pronotum similar to or a little weaker than those on head, systematic punctures well marked, 3–4x diameter of adjacent punctures, rear and lateral margins weakly grooved and flanged, front margin grooved to about level of inner edge of eyes. Elytral punctures as on pronotum, more weakly impressed towards rear. Serial punctures in four loose rows, sparse and indistinct, more numerous but more scattered laterally, elytra weakly grooved and flanged laterally. Mesosternal pillar well marked, triangular in both front and lateral views, posterior edge often steeper near top of keel, reaching a short distance between mesocoxae.

Male: Aedeagus very short, broad, rounded, lacking narrower apical section. Parameres squat, inner edge a little sinuate, tips obliquely truncated

on inside or curved weakly outwards. Proclaw straightened with strong basal swelling, mesoclaw thickened, curved with basal swelling, metaclaw straightened and greatly swollen in basal half. In female claws similar but with straightening and basal swelling much weaker.

Distribution

Known only from the type localities in North Queensland and the Northern Territory.

Remarks

Readily separated from all other Australian *Enochrus (Methydrus)*, other than *E. eubenangeei*, by its large size and almost all-black colouring. The very short, broad aedeagus, and weak lateral punctures on the elytra separate it from the otherwise very similar *E. eubenangeei*.

In general appearance it is similar to *E. (H.) mastersi* but readily separated by its longer maxillary palpi with the apical segment shorter than penultimate. See also under remarks in *E. mastersi*.

Enochrus (Methydrus) deserticola (Blackburn)

Philhydrus deserticola Blackburn, 1896

Enochrus (Lumetus) deserticola (Blackburn):
Knisch 1924

=*Enochrus mjobergi* Knisch, 1921: syn. nov.

=*Enochrus (Lumetus) mjobergi* Knisch: Knisch 1924

=*Philhydrus temporalis* Régimbart, 1908: syn. nov.

=*Enochrus (Lumetus) temporalis* (Régimbart):
Knisch 1924

Types

Enochrus deserticola: *Lectotype*: '5487, Bl. Paisley T' top specimen of two separately carded on same pin, BM(NH), herein designated.

Paralectotypes: 1 unlabelled but mounted below lectotype on same pin, BM(NH); 1 ♂ '5487 Palm Cr', '*Philhydrus deserticola* Blackb. Co-type', SAMA; 3, 'Reedy Hole', NMV; 2, 'Ellery Ck', NMV; 2, 'Paisley Bluff', NMV.

Enochrus mjobergi: *Lectotype*: ♂ 'Cape York Penins'; 'Queensl. Mjöberg'; 'Type', '*Enochrus (Lum.) mjobergi* m. n. sp., A. Knisch 1921'; 'Typus', on red label NRS, herein designated.

Paralectotypes: 1, 'Queensl. Mjöberg Cape York Penins'; 'Sjöstedt don 1921'; 'Ex Coll. Knisch No. 5521544 Coll. d'Orchym'; 'Knis det

Enochrus (L.) *mjöbergi* m'; Coll. A. Knisch TYPUS', on red card. IRSNB; 3, 'Cape York Penins'; 'Queensl. Mjöberg', NRS. Synonymy after examination of types.

Enochrus temporalis: Holotype: 'Avon R'; 'eaudouce'; '*Philhydrus temporalis*, Reg. TYPUS', MNHN. Synonymy based on descriptions and examination of types (of *E. temporalis* in 1964, not currently available).

Description (number examined, >1000) Fig. 4

Oblong oval, length 3.3 mm – 4.9 mm. Two colour morphs; one with dorsal surface black except light portions in front of eyes, other with elytra and pronotum light testaceous and head dark testaceous to black except for light testaceous area forward from eyes and a little wider than eyes, leaving central darker panel of variable width on front of head, underside dark testaceous, appendages lighter towards extremities except for maxillary palpi which usually have apical portion of last segment darker. Head covered with small, sharply impressed, well separated punctures a lot smaller than eye facets, a group of large punctures inwards from each eye, at least 4x diameter of other punctures. Punctures on pronotum as on head, but more shallowly impressed, systematic punctures as in *E. elongatus*, four or more times diameter of adjacent punctures. Elytral punctures increase somewhat in strength apically and laterally, serial punctures large, sparse and quite distinct at apex, interstitial punctures varying from weak to almost obsolete.

Mesosternal keel well developed, front edge nearly perpendicular, ventral edge straight or slightly convex.

Male: Aedeagus pointed, with weak dorsal pad at tip, collar a bit closer to tip than base. Parameres outwardly hooked at tips. Proclaw with basal lobe and rest of claw somewhat straightened. Meso- and metac claws, with slight basal lobes, weakly curved.

Female: Claws only slightly weaker than males.

Distribution

New South Wales

Bonville, ANIC; Chichester SF, ANIC; Clarence River, NMV; Coff's Harbour, ANIC; Fowlers Gap, ANIC; 10 km N Jabiru, QDPIM; Lord Howe Island, SAMA; Moree, SAMA; Valcry, ANIC; Wootton, ANIC.

Northern Territory

Adelaide River, ANIC; E Alligator River, AM; Bessie Spring, ANIC; Berry Spring, ANIC; 45

km SW by S Borroloola, ANIC; 7 km NW by N Mt Cahill Crossing East Alligator River, ANIC; 8 km N Mt Cahill, SAMA; 12 km NNW Mt Cahill, SAMA; 14 km S by W Cape Crawford, ANIC; Cooper Creek, ANIC; Daly River Mission, ANIC; 170 km E Daly Waters, SAMA; Darwin, ANIC, SAMA; Ellery Ck, NMV; 15 km S Elliot, SAMA; Harst Bluff, NMV; 12 km NE Humpty Doo, QDPIM; Jim Jim Creek, ANIC; Koogarra, ANIC; 4 km N McArthur R Stn, SAMA; 19 km SSE Mataranka, SAMA; 5 km E Mataranka, SAMA; Nourlangie Creek, ANIC; 18 km E by N Oenpelli, ANIC; Paisley Bluff, NMV; Pine Creek, QDPIM; Reedy Hole, NMV; 46 km S Renner Springs, SAMA; Stanley Chasm, SAMA, ANIC; 100 km W Tennant Creek, QDPIM; Tindal, ANIC; Wessel Island, ANIC.

Queensland

Ashmore, QM; Atherton, ANIC, QDPIM; 31 km NE Aramac, SAMA; Bakerville, QDPIM; Bamaga, SAMA; Brisbane, QM, UQIC; Benaraby, ANIC; 5 mls N Bloomfield River, ANIC; Bundaberg, ANIC; Bunya Mts, ANIC; Burketown, QM; Cairns, ANIC, SAMA; Calliope River, ANIC; Camooweal, QDPIM; Cape Tribulation, ANIC; Cardstone, ANIC; Chillagoe Creek, ANIC, QDPIM; Coen, QDPIM; 60 km S Coen, SAMA; Mt Coolum, ANIC; Cooktown, ANIC; 30 mls N Cooktown, UQIC; Crystal Creek, ANIC; Cunningham's Gap, ANIC; Dalhenty River, SAMA; Edungalba, ANIC; 5 km NE Edungalba, SAMA; Eidsvold, ANIC; Emu Park, UQIC; Fletcher, QM; Gayndah, UQIC; Mt Garnet, ANIC; Greenhills, ANIC; Home Hill, QDPIM; Ingham, ANIC, SAMA; Mt Inkerman, ANIC; Iron Rng, QDPIM; Julatten, ANIC; Julia Creek, SAMA; Kenilworth SF, UQIC; Kingaroy, ANIC; Kuranda, ANIC, SAMA; Laura, QDPIM; 70 km N Laura, QDPIM; 25 km N Laura, QDPIM; Mt Lewis, ANIC; Mackay, ANIC; Magnetic Isl, SAMA; Malanda, SAMA; 23 km E Mareeba, QDPIM; Mary Creek, ANIC; Melvor, ANIC; 21 mls S Miriam Vale, ANIC; 100 mls S Miriam Vale, UQIC; Mission Beach, ANIC; 3 mls W Mourilyan, ANIC; Mornington Isl mission, SAMA; 5 km W Mossman, QM; Mossman George Nt Pk., UQIC; Mossman George, ANIC; Normanton, QDPIM; Oxley Ck, QM; Paluma Dam, ANIC; 9 km W Paluma, QDPIM; Prince of Wales Isl, NMV; 8 mls NE Proserpine, ANIC; Rocklea, QM; Stanthorpe, QM; Mt Spec, ANIC; Stewart Rng, SAMA; Tolga, SAMA; Townsville, ANIC, NMV, SAMA; 9 km ENE Mt Tozer, ANIC; Weipa, QDPIM;

Windsor Tableland, QDPIM; Yamba, UQIC; Yungaburra, QDPIM.

South Australia

Arkaba Creek, SAMA; Mambray Creek, SAMA; Marne River, SAMA; Mt Remarkable, SAMA; 6 km E Nilpinna, SAMA.

Victoria

Dimboola, ANIC; Genoa, ANIC; Sea Lake, SAMA.

Western Australia

6 km NNW Broome, ANIC; Beverley Springs, WAM; Cadjeput Rockhole, WAM; Charnley River, 25 miles N Beverley Springs, WAM; Derby, SAMA; Drysdale River, ANIC; 7 miles NE Giles, WAM; Gill Pinnacle, WAM; Hammesley Rng, SAMA; Koolan Island, WAM; 6.5 km N Mt Bell, WAM; Kununurra, ANIC, QDPIM; Millstream, ANIC; 5 km SE Millstream HS., ANIC; Mitchell Plateau, ANIC; West Peewah River, ANIC; Synnott Range, WAM; 14°53'S, 125°45'E, SAMA.

Remarks

A relatively large species showing considerable variation in size, colour and strength of dorsal punctation making its identification difficult without dissection. The two colour morphs are well marked and occur together in the same populations. Occasional specimens have an intermediate dark-testaceous dorsal surface to a variable extent. It is my impression that the dark form is more common in the north where it is the dominant form in many areas. The black morphs are readily identified by their weak to moderate punctation contrasting markedly with the strong punctation in the two other species with black morphs, *E. eyrensis* and *E. samae*. It is also the only species with the combination of tips of the parameres hooked, weak to moderate dorsal punctures and black patterning on the head. In the North-east the species overlaps with *E. weiri* and *E. pseudoweiri*. These can be separated from most *E. deserticola* by the lack of black morphs, somewhat stronger punctation, pale tips to the maxillary palpi and the small amount of black on the front of the head. An occasional specimen of *E. deserticola* may also have pale palpi tips and much reduced black on the front of the head.

Over most of its range *E. deserticola* is sympatric with *E. maculiceps*. The two species are readily separated by the male genitalia and presence of black morphs in *E. deserticola*. I

have, however, been unable to reliably separate light coloured females. In general *E. deserticola* are larger and more weakly punctured but considerable character overlap occurs between the two species.

In more southern areas *E. deserticola* overlaps with *E. eyrensis*, *E. samae* and *E. elongatus* but can be separated from all three by the much weaker punctation and in the case of *E. elongatus* by the well-marked dark patterning on the head which *E. elongatus* lacks.

Enochrus (Methydrus) elongatus (W. MacLeay)

Philhydrus elongatus W. MacLeay, 1873

Enochrus (Lumetus) elongatus (W. MacLeay)
Knisch, 1924

= *Philhydrus caledonicus* Fauvel, 1883: syn. nov.

= *Enochrus caledonicus* (Fauvel): Knisch, 1924

Types

Enochrus elongatus: Lectotype: 'Philhydrus elongatus Gayndah McL W'; 'KI9506'. Right-hand specimen of two mounted on same card, AM herein designated.

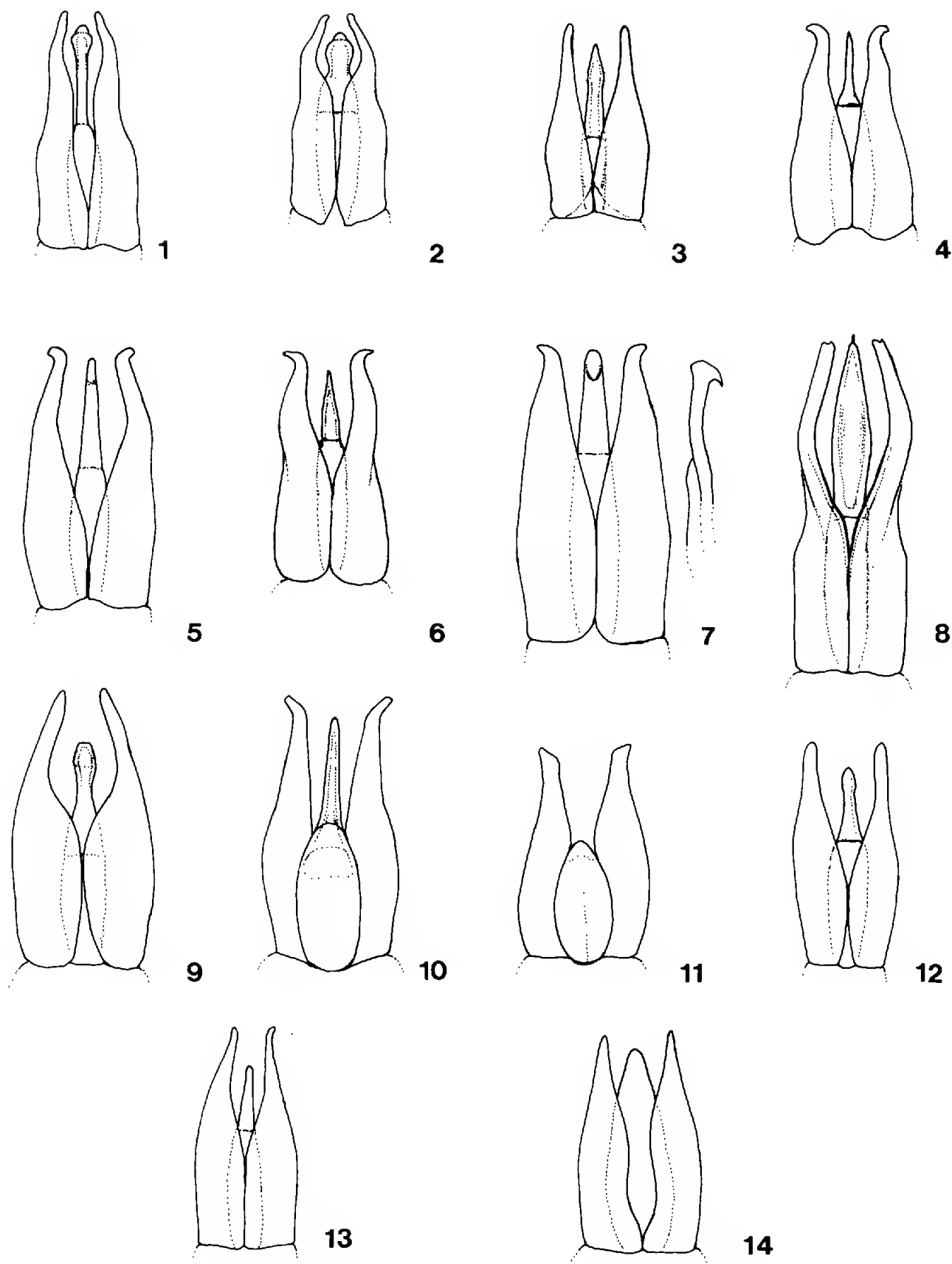
Paralectotypes: 1, same data as lectotype, left-hand specimen, AM; 3, on same card, same data as lectotype, ANIC; 1, 'Philhydrus elongatus McL', 'Griffith Collection Id by A. M. Lea', 'Co-Type', SAMA; 1, 'Philhydrus elongatus M. Queensland cotype 14629', SAMA.

Enochrus caledonicus: Lectotype: 'm', 'Nouvelle Calédonie. Noumea Marais Anse Vata, Octobre Savés, ex. coll. Fauvel', 'Coll. et det. A. Fauvel Philhydrus caledonicus Fvl', '17-479', 'lectotype' on red label. Remounted with genitalia dissected out, IRSNB.

Paralectotypes: 1, 'Nouvelle Calédonie Kanala, Rec. Coste, ex coll. Fauvel'; 'Coll. et det A. Fauvel Philhydrus caledonicus Fvl.' '17-479', 1, 'Nouvelle Calédonie. Anse Vata, Nouméa Savés', 'Coll. et det A. Fauvel Philhydrus caledonicus Fvl', IRSNB. Synonymy after examination of types.

Description (number examined, 330) Fig. 7

Elongate oval, body flattish, length 4.4 mm – 5.0 mm. Dorsal surface testaceous, diffusely blotched, lighter towards sides, rear of head often diffusely darker but never distinctly darker than rest of head. Ventral surface dark red-brown, apical portions of legs lighter, palpi light testaceous, tips of maxillary palpi dark brown. Head covered with small sharply impressed, well



FIGURES 1-14. Dorsal views of apical portion of male genitalia. 1 & 2, *E. maculiceps* showing range of variation; 3, *E. pseudoweiri*; 4, *E. deserticola*; 5, *E. eyrensis*; 6, *E. isabellae*; 7, *E. elongatus*, lateral view of median lobe; 8, *E. weiri*; 9, *E. samae*; 10, *E. eubenangeei*; 11, *E. aliciae*; 12, *E. malabarensis*; 13, *E. esuriens*; 14, *E. mastersi*.

separated punctures, quarter to half size of eye facet, a dozen or so much larger punctures inwards from each eye. Pronotum similarly punctate, a row of systematic punctures about 3x diameter of adjacent punctures running inwards from each front corner and smaller group of similar punctures a little behind middle on each side. Elytral punctures slightly stronger than those on pronotum, stronger laterally than on disc. Serial punctures, larger, sparse, hard to trace towards apex. Underside evenly setose-punctate, rugose portions of femur, approximately three quarters length of femur. Mesosternal keel well developed, anterior edge curved somewhat, nearly perpendicular, ventral edge flat or slightly convex. Notch on apical sternite small but well marked.

Male: Aedeagus with crotchet-shaped hook at tip. Tips of parameres outwardly hooked. Metac claws with enlarged basal lobe and rest of claw straightened. Pro- and mesoclaw curved with thickened basal portion.

Female: Claws curved with thickened basal portions.

Distribution

Australian Capital Territory

Black Mt, ANIC.

New South Wales

Albury, ANIC; Allyn River, NMV; Armadale, ANIC; Balranald, ANIC; Bathurst, AM; Bogan River, AM; 20 mls SSW Bourke, SAMA; Broken Hill, SAMA; Coonabarabran, AM, ANIC; Cowra, AM; Ecclestone, AM; Hay, ANIC; 37 km E Hay, SAMA; Mt Kaputar Nat. Pk., ANIC; Kosciusko Nt Pk., ANIC; Lake Menindie, SAMA; Menindie, SAMA; Narrabri, ANIC; Norfolk Island, ANIC; 97 km S Tibooburra, NMV.

Northern Territory

53 km NE Alice Springs, ANIC; 12 km SW by W Alice Springs, ANIC; Top of Ayers Rock, WAM; 97 km N Barrow Ck, SAMA; 30 km NE by E Borroloola, ANIC; Ellery Creek, NMV; Finke, SAMA; Glen Helen, NMV; Stanley Chasm, ANIC; 15 km East, Vaughan Spring, HS, ANIC.

Queensland

Bollon Dist, AM; 42 km Boulia, ANIC; Bunya Mts, UQIC; Camooweal, QDPIM; Edgbaston HS, SAMA; 5 km NE Edungalba, SAMA; Glen Alpin, UQIC; Helidon, UQIC; 6 km E, Kamma, ANIC; Mackay, ANIC; MacPherson Rng, Nt Pk., AM; Marmor, ANIC; Mt Isa, QDPIM; Mt Spec,

ANIC; Normanton, QDPIM; Tolga, QDPIM; Toowoomba, UQIC.

South Australia

Aroona Dam, SAMA; Mt Barr, ANIC; Old Billa Kallina HS, SAMA; Blanche Cup Spring, AM; Broken Hill, AM; Coopers Creek, SAMA; Coward Sp., SAMA; 16 km E Curdimurka, SAMA; 36 km ESE Curdimurka, ANIC; 11 km NE by Etadunna HS, ANIC; Gawler Rngs, SAMA; Lake George, ANIC; Mt Lofty Rng, AM; Mannum, SAMA; Marne River, SAMA; McDovall Peak, UQIC; Murray Bridge, AM, SAMA; Olary, ANIC; Oodnadatta, SAMA; Paralana Hot Springs, SAMA; Quorn, AM; Renmark, SAMA; Roonka Stn, SAMA; Roseworthy, SAMA; Scorpion Springs CP, SAMA; River Torrens, SAMA; Warburton, River, ANIC; Wearing Gorge, SAMA; Willochra Ck, SAMA.

Tasmania

15 m N Waratah, UQIC.

Victoria

Eppalock Res., NMV; Eustace Gap Ck, NMV; King Lake Nt Pk., NMV; Kiata, NMV; La Trobe River, NMV; Lake Hattah, ANIC; Lilydale, SAMA; Little Desert, ANIC; Lake Hattah, NMV; Marysville, SAMA; Melbourne, UQIC; Preston, NMV; Shepparton, ANIC; Skeleton Ck, SAMA; Stawell, SAMA; Swan Hill, NMV; Traralgon Ck, NMV; Violet Town, ANIC; East Warburton, NMV; Wyperfeld Nt Pk, ANIC.

Western Australia

15 km SSE Armadale, ANIC; 102 km SE by E, Broome, ANIC; 12 km NE Broome, ANIC; Bunbury, ANIC; 23 km NW by W Mt Arid, ANIC; 7 miles NE Giles, WAM; Gill Pinnacle, WAM; Great Victoria Desert, WAM; Mary sp. HS, ANIC; 13 km ESE Mooka H.S., WAM; Koolan Island, WAM; Serpentine River, NMV; West Peawah River, ANIC; Wilga, ANIC; Wingello, ANIC.

Remarks

Enochrus elongatus differs from all other Australian *Enochrus* by the pale coloured dorsal surface including the head. It is the only Australian species with the tip of the aedeagus distinctly hooked upwards and with a basal swelling on the meta- and mesoclaw as well as the proclaws.

The rear of the head is variably coloured. In many specimens it is darker than the front of the

head, but diffusely so and never black and sharply delineated from the front as in most other species.

Enochrus elongatus superficially resembles the pale morphs of *E. deserticola* and *E. eyrensis* in size and colour. It also shares with them, and no other Australian species, the hooked parameres. Unlike them the black colour morph common in these two species does not appear to occur in *E. elongatus*. In both *E. deserticola* and *E. eyrensis* the head is predominantly black with only small patches of yellow-brown on the front angles. In *E. elongatus* the head is uniformly yellow-brown or the rear is diffusely darker. In *E. deserticola* the dorsal punctation is much weaker than in *E. elongatus* and in *E. eyrensis* it is stronger.

Enochrus elongatus is a widespread and common species within Australia including Norfolk Island. I can find no significant difference between Australian specimens and the types of *E. caledonicus* thus extending the range of *E. elongatus* to New Caledonia.

***Enochrus (Methydrus) esuriens* (Walker)**

Philhydrus esuriens Walker, 1858

Enochrus (Lumetus) esuriens (Walker): Knisch 1924

Enochrus (Methydrus) esuriens (Walker): d'Orchymont 1927

= *Philhydrus pullus* Fauvel, 1883: syn. nov.

= *Enochrus (Lumetus) pullus* (Fauvel): Knisch 1924

Types

Enochrus esuriens: Type locality: Ceylon (Sri Lanka). Type not seen.

Enochrus pullus: Lectotype: ♂ 'Coll. IRSNB, Nouvelle Calédonie, Anse Vata, Marais Juill Octobre Rec. Savés, ex. coll. Fauvel'; 'Coll. et det A. Fauvel *Philhydrus pullus* Fvl. IRSNB 17-497', IRSNB with red lectotype label, herein designated. Scen.

Paralectotypes: 3 ♂, 1 ♀, same data as lectotype in IRSNB.

I have not seen type material of *E. esuriens* and have relied on the work of Balfour-Browne (1939, 1945) and specimens identified by him in BM(NH) for my concept of this widespread species which is known from India, through South-East Asia to Northern Australia and Polynesia.

Description (number examined, 130) Figs 13, 18
Length 1.6 mm – 2.3 mm. Oblong-oval. Elytron

and pronotum light-testaceous, often blotched and streaked darker, head black, area in front of eye, to about width of eye light-testaceous, central black panel two to three times width of lateral light area. Ventral surface dark-testaceous, appendages lighter towards extremities, whole of apical segment of maxillary palpi usually darker. Punctures on head moderately strong, systematic punctures inwards from eyes about size of eye facet and about twice diameter of adjacent punctures. Punctures on pronotum somewhat weaker, punctures on elytra somewhat stronger than on head, those towards apex and laterally about half diameter of adjacent serial punctures which are often not easy to trace. Mesosternal keel weakly developed.

Male: Aedeagus narrow, pointed, virtually lacking terminal dorsal pad, shorter than parameres, collar nearer base than tip, parameres broad in basal half narrow for most of apical half, inner edge only very weakly sinuate, tips rounded. Proclaw straightened, strongly swollen at base, meso- and metac claws rounded, swollen at base.

Distribution

New South Wales

Wootton, ANIC.

Northern Territory

Adelaide River, ANIC; E Alligator River, AM; Darwin, ANIC; Humpty Doo, QDPIM; 12 km N Humpty Doo, QDPIM; 6 km N Humpty Doo, QDPIM; Jim Jim Creek, ANIC; 9 km N by E Mudginbarry HS, ANIC; 19 km E by S Mt Borradaile, ANIC; 12 km NNW Mt Cahill, ANIC; Nourlangie Creek, ANIC; Oenpelli, AM.

Queensland

Annan Falls, ANIC; Ayr, ANIC; 29 km S Bamaga, ANIC; Cairns, ANIC, SAMA; Calliope River, ANIC; Cardstone, ANIC; 60 km S Coen, SAMA; 40 km N Coen, SAMA; Ingham, ANIC; Lansdowne St, ANIC; 73 km NW Laura, ANIC; Laura, QDPIM; Macleod River, SAMA; Mackay, ANIC; Mareeba, QDPIM; Mary Creek, ANIC; Mt Baird, ANIC; Mt Coolum, ANIC; Mt Ivor River, ANIC; Mt Molloy, ANIC; 2 km NNE Mt Tozer, ANIC; 11 km ENE Mt Tozer, ANIC; 8 km E by N of Mt Tozer, ANIC; 12 km S Normanton, SAMA; North Pine River, UQIC; Port Douglas, ANIC; Redcliff, UQIC; 15 km WNW South Johnstone, QDPIM; Townsville, ANIC, SAMA; Weipa, QDPIM.

Western Australia

Mitchell Plateau, ANIC; Nullagine, WAM.

Remarks

Enochrus esuriens' small size (<2.5 mm), predominantly black head and weak mesosternal keel make it one of the most readily recognised species of Australian *Enochrus*. It is most easily confused, not with other *Enochrus*, but with species of *Paracymus* and *Anacaena*. These latter genera lack the systematic punctures present on the head, pronotum and elytra of *Enochrus*.

Enochrus (Methydrus) eubenangeei* sp. nov.*Types**

Holotype: ♂, 'Qld. Babinda Eubenargee Swamp, 1/4/96, C. Watts', SAMA.

Paratypes: 6, 'Bramston Beach via Innisfail, N.Q., 15 Aug. 1987, A. Walford-Huggins, coastal melaleuca swamp at light', ANIC; 1, 'N.T. Corndorl billabong nr. Jabiru, M.V. light, 2.x.1982, M.B. Malipatil', NTM.

Description (number examined, 8) Fig 10

Length 7.0–7.5 mm. Broadly oval, relatively flat. Shiny. Black; palpi and tarsi testaceous. Maxillary palpi moderately long, pseudo first segment longer than distance from eye to front of clypeus, longer than maxillary stipe, apical segment approximately three-quarters length of penultimate. Head strongly punctate, most punctures about a puncture width apart, almost size of eye facet. Systematic punctures large, about 3x size of adjacent punctures. Punctures on pronotum well marked, similar to those on head, not greatly weaker laterally, systematic punctures well marked about 3x size of adjacent punctures, lateral margins grooved and flanged, front and rear margins weakly grooved. Elytral punctures as on pronotum, not greatly weaker laterally. Serial punctures in four loose rows, relatively well marked, more numerous but more scattered laterally, elytra weakly grooved and flanged laterally. Mesosternal pillar well marked, sharply triangular in front view, front edge sloping, ventral edge short slightly pointed at rear, rear edge vertical in top half. Notch on apical sternite shallow, relatively broad.

Male: Aedeagus with very broad basal portion and narrow apical portion which is curved upwards. Parameres relatively broad, hooked outwards at tips, bent upwards in apical half. Proclaws bent, broadly thicker in basal third,

thickened part ends abruptly, meso- and metaclaws curved, basal third somewhat thickened, thickened part ending smoothly.

Remarks

Enochrus eubenangeei closely resembles *E. aliciae*. Apart from the genitalia it differs from *E. aliciae* in the lateral punctures on pronotum and elytra being almost as strong as more central ones and a greater extent of black. Based on the relatively few specimens of both species that are available *E. eubenangeei* also differs from *E. aliciae* by its black head, whereas in many *E. aliciae* the head has some testaceous colour, and by the broader but narrower exposure of the membrane between frons and clypeus than in *E. aliciae* where it is shorter but deeper.

The aedeagi are distinct. *Enochrus eubenangeei* has a normal narrow apical portion to the aedeagus, without apical pad but bending strongly upwards. *Enochrus aliciae* has a very broad basal portion but, uniquely among Australian *Enochrus*, lacks the apical portion, resulting in the aedeagus reaching little beyond half way along the parameres. The parameres are rather similar but the tips are more obviously hooked in *E. eubenangeei* and they bend noticeably upward in this species.

In its relatively large size, rounded shape and shiny, black appearance, *E. eubenangeei* also resembles *E. mastersi*. It, and *E. aliciae*, can be most readily separated from this more common species by the longer maxillary palpi with the apical segment shorter than the penultimate. The only other species it could be confused with is *E. isabellae* which is smaller, narrower, has light areas in front of its eyes and has the mesosternal process long and blade-like.

Distribution

Known only from type localities in Northern Territory and Queensland.

***Enochrus (Methydrus) eyrensis* (Blackburn)**

Philhydrus eyrensis Blackburn, 1894

Enochrus (Lumetus) eyrensis (Blackburn):

Knisch 1924

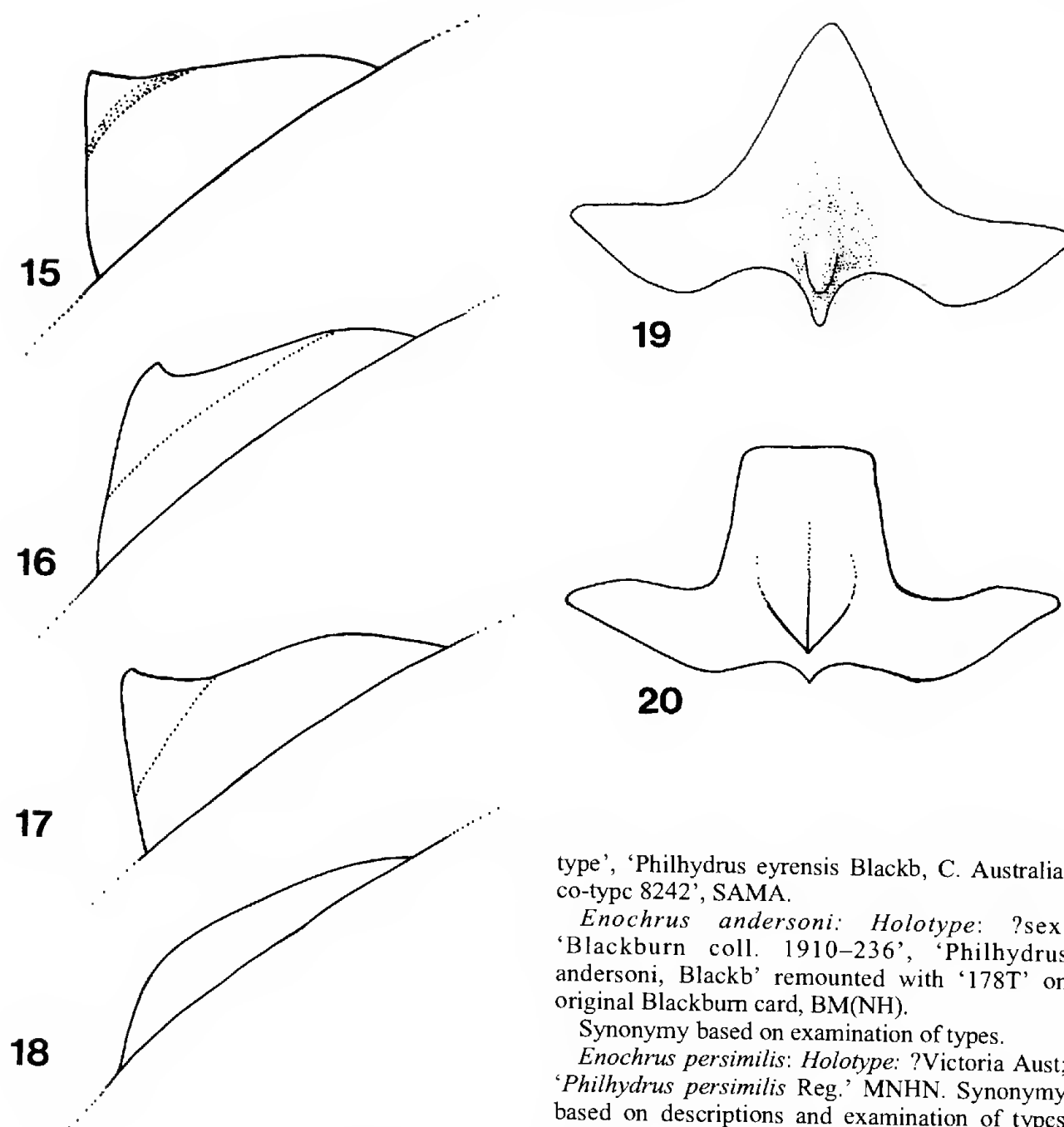
= *Philhydrus andersoni* Blackburn, 1896: syn. nov.

= *Enochrus (Lumetus) andersoni* (Blackburn):

Knisch 1924

? = *Philhydrus persimilis* Régimbart, 1908: syn. nov.

? = *Enochrus (Lumetus) persimilis* (Régimbart): Knisch 1924



FIGURES 15–20. Mesosterna. 15–18, Lateral view of mesosternal keel. 15, *E. samae*; 16, *E. eyrensis*; 17, *E. maculiceps*; 18, *E. esuriens*. 19 & 20, mesosternum. 19, *E. mastersi* (after Hansen 1990); 20, *E. aliciae*.

Types

Enochrus eyrensis: Holotype: ♀, 'Blackburn coll. 1910–236', 'Philhydrus eyrensis Blackb', remounted with '178T' on original Blackburn card, BM(NH),

Paratypes: 2 'Philhydrus eyrensis Blackb co-

type', 'Philhydrus eyrensis Blackb, C. Australia, co-type 8242', SAMA.

Enochrus andersoni: Holotype: ?sex. 'Blackburn coll. 1910–236', 'Philhydrus andersoni, Blackb' remounted with '178T' on original Blackburn card, BM(NH).

Synonymy based on examination of types.

Enochrus persimilis: Holotype: ?Victoria Aust; 'Philhydrus persimilis Reg.' MNHN. Synonymy based on descriptions and examination of types (of *E. persimilis* in 1964, type not currently available). It is possible that my *E. samae* will prove to be this species.

Description (number examined, 146) Figs 5, 16

Oblong-oval, length, 3.2 mm – 5.0 mm. Two colour morphs exist, one with elytra and pronotum testaceous often with sutural lines and striae darker, occasionally with disc of pronotum darker, head dark-testaceous to black with lighter area forward from eyes to about the same width as eyes giving a darker central panel three to four times the width of one of the lighter patches, clypeus dark. Second colour morph has the elytra dark-testaceous or black, pronotum a

similar colour but quite widely but diffusely lighter laterally, head as for first colour morph. Underside of both morphs dark-testaceous, appendages lighter towards extremities, except for maxillary palpi which have apical portion of apical segment darker.

Head quite densely covered with relatively strong punctures about half size of eye facet, a few large punctures inwards from eyes, 2–3x diameter of surrounding punctures. Punctures on pronotum slightly stronger, systematic punctures as in *E. elongatus*, 2–3x diameter of adjacent punctures. Punctures on elytra rather stronger than on pronotum, towards apex approaching size of scial punctures, which, as a consequence, are hard to trace.

Mesosternal keel well developed, anterior edge weakly curved, nearly perpendicular, ventral edge straight or weakly convex, narrow vertical 'blade' above an extensive broader base. Notch on apical sternite moderately developed.

Male: Aedeagus narrow, pointed, virtually lacking terminal dorsal pad, collar nearer base than tip. Parameres outwardly hooked at tip. Proclaw a little longer, less curved than in female, otherwise little sexual difference in claws.

Distribution

Australian Capital Territory

Black Mt, ANIC; Jarvis Bay, ANIC.

New South Wales

Bonville, ANIC; 25 km N Bulahdelah, ANIC; Maroota South, ANIC; 8 km SE by S Moruya, ANIC; Norfolk Island, ANIC; Queanbeyan, ANIC; 17 mls S Woodburn, ANIC; Wootton, ANIC.

South Australia

Adelaide, SAMA; American River, SAMA; Beachport, AM, SAMA; Bool Lagoon, SAMA; Coonalpyn, SAMA; Fairview Park Cons Pk, SAMA; Hindmarsh Park, SAMA; Lucindale, SAMA; Naracoorte, UQIC; Taratap Stn, SAMA.

Tasmania

Scamanden River, NMV; Swansea, SAMA.

Victoria

East Pomborneit, ANIC; Lorne, SAMA; Maffra, UQIC; Otway Rngs, UQIC; Wyperfeld Nt Pk, ANIC.

Western Australia

Albany, ANIC; Applecross, ANIC; Broomehill,

WAM; Dumbleyung, WAM; 5 km NE Esperance, ANIC; 63 mls E Esperance, ANIC; 9 mls NE by N Esperance, ANIC; 19 km E Esperance, ANIC; 5 km NW Esperance, ANIC; Fitzgerald River Nt Pk, ANIC; Karridale, ANIC; Maidavale, SAMA; Mt Margaret, ANIC; Mandurah, ANIC; 23 km NW by N Mt Arid, ANIC; Perth, ANIC; 8 mls E Pinjarra, ANIC; Stirling Rngs, SAMA; 12 km NE Wanneroo, WAM; 155 km SW Warburton, WAM; Wilga, ANIC.

Remarks

This relatively large species is common in both the south-east and south-west.

The relatively strong dorsal punctation separates it from all other Australian *Enochrus* except *E. samae* and the generally much smaller *E. malabarensis*. *Enochrus malabarensis* is also a more northern species and lacks black morphs. From *E. samae*, *E. eyrensis* differs in having the parameres hooked at the tips rather than rounded and in a higher, more blade-like mesosternal keel. This latter character is, I believe, a good one but is hard to see on many specimens and is difficult to use if comparative material is not available.

Enochrus eyrensis appears close to *E. tristis* (Broun) from New Zealand and some Pacific Islands in the hooked parameres and strong punctations. It differs from this species in having the apical portion of the aedeagus shorter than the basal and in rounded, not slightly straightened, male metac claws. *Enochrus eyrensis* differs from *E. abditus* (Sharp) from New Zealand, in details of the aedeagus and mesosternal keel.

Enochrus (Methydrus) isabellae sp. nov.

Types

Holotype: ♂, right-hand specimen on card, 'Qld. Townsville, 10 km NW, 23/3/96, C. Watts', SAMA.

Paratypes: 7, same data as holotype, SAMA; 3, 'Ayr Qld., 10.ix.1990, W.B. Muir', in ANIC; 1, 'Ingham, N.Q., 27.i.68, J.C. Brooks', ANIC; 1, 'Blighs Lookout, Cardwell Rng, N.Q. at light, 30.ix.67, J. Brooks', ANIC; 1, 'Bramston Beach via Innisfail, N.Q., 15.viii.1987, A. Walford-Huggins. Coastal mclaleuca swamp at light', in ANIC; 6, 'Qld. Nardello's Lagoon nr. Mareeba 29/3/96, C. Watts', SAMA.

Description (number examined, 14) Fig 6

Length 4.5 mm – 5.5 mm. Oval, shiny. Black apart from lateral areas of pronotum, region in

front of eyes and appendages which are reddish-yellow. Tips of maxillary palpi darker. Head quite densely punctate, with weak to moderately sized punctures, systematic punctures rather sparse, somewhat larger than an eye facet and 2–3x size of adjacent punctures. Pronotum and elytra similarly punctured except that systematic punctures a bit larger in comparison with others. Mesosternal keel well-developed, narrow, often with small protuberance on anterior end.

Male: Claws on protarsi more bent than in female with broad basal portion. Parameres hooked apically, aedeagus with apical portion shorter than basal, relatively broad, narrowing rapidly at tip, slight but noticeable dorsal thickening at tip.

Distribution

Known only from type localities in Queensland.

Remarks

A relatively large nearly totally black species. It strongly resembles the black morphs of *E. eyrensis* and *E. samae* but is much more weakly punctured, has a shorter apical portion of the aedeagus than in *E. eyrensis* and has hooked parameres which distinguish it from *E. samae*. Compared to the black morph of *E. deserticola* which occurs sympatrically with it, it is larger, more strongly punctured and has more extensive black on the front of the head than is normal in *E. deserticola*. The male genitalia are relatively similar to those of *E. deserticola* but *E. isabellae* has a broader and shorter apical portion to the aedeagus with a more developed apical dorsal/ventral thickening. From *E. elongatus* it can be separated on colour, generally weaker punctuation, weaker apical hook on aedeagus which ends well short of tips of parameres and lack of modified meso- and meta-claws in the males.

The Townsville and Nardello's Lagoon specimens were collected from shallow water among thick drying reeds at the edge of extensive shallow swamps.

Enochrus (Methydrus) maculiceps (MacLeay)

Philhydrus maculiceps MacLeay, 1873

Enochrus (Lumetus) maculiceps (MacLeay):
Knisch 1924

= *Philhydrus laevigatus* Blackburn, 1888: syn. nov.

= *Enochrus (Lumetus) laevigatus* (Blackburn):
Knisch 1924

= *Philhydrus artensis* Fauvel, 1883: syn. nov.

= *Enochrus (Lumetus) artensis* (Fauvel): Knisch 1924

= *Enochrus (Lumetus) bryani* d'Orchymont, 1927: syn. nov.

Types

Enochrus laevigatus: *Holotype*: 'Philhydrus laevigatus Blackb', BM(NH), 'Blackburn coll. 1910–236'. Remounted with '1552T' on original Blackburn label. Synonymy based on examination of types.

Enochrus maculiceps: *Lectotype*: Male. 'Philhydrus maculiceps McL. W. Gayndah', 'K19505'. Right-hand specimen of two mounted on same card, AM, herein designated.

Paralectotypes: 1, on same card as lectotype, AM; 2, same data as lectotype and mounted on one card, in ANIC; 'Philhydrus maculiceps McL. 'Co-type' Griffith collection id by A.M. Lea'; 1, 'Philhydrus maculiceps McL. Queensland co-type 14631', SAMA. Synonymy based on examination of types.

Enochrus artensis: *Holotype*: 'Nouvelle Caledonie Ile Art', 'Rec. ex. coll. Fauvel', 'Coll. et det. A. Fauvel *Philhydrus artensis* Fvl', with red Holotype label, IRSNB.

Paratype: ♀, 'Nouvelle Caledonie Kanata Re Deplenche ex. coll. Fauvel'; 'Coll. et det. A. Fauvel *Philhydrus artensis* Fvl, IRSNB 17–479', with orange paratype label, IRSNB. Synonymy based on examination of types.

Enochrus bryani: *Holotype*: 'Savaii Samoa', 'Salailua v-22–24', 'H. Bryan Jr, Collector', ♂, 'Type', 'A. d'Orchymont det, *Enochrus (Lumetus) bryani*', Bishop Museum, Honolulu.

Paratype: '*Enochrus (Lumetus) bryani* A. d'Orchymont det'; 'Samoan Is. Apia Upolu Is'; 'female' 'I Samoa Mars 1924 Coll. d'Orchymont', IRSNB.

Both the types are mounted on card from the same source and similarly labelled by d'Orchymont. d'Orchymont clearly identified the Bishop Museum specimen as the holotype. Unfortunately all but a hind tibia and tarsus of the holotype has been lost. I base my concept of *E. bryani* on the Brussels paratype and d'Orchymont's description and illustration of the aedeagus.

Description (number examined, 134) Figs I, 2, 17

Length 2.6 mm – 4.0 mm. Elytra testaceous, sutural lines, some serial punctures and a rough, small patch on each humeral angle darker; pronotum testaceous, disk rather darker than sides; head with testaceous areas in front of each

eye much wider than eye, central dark panel about half width of lateral light patches, boundary between areas often diffuse. Ventral surface dark-testaceous, appendages only slightly lighter towards extremities, maxillary palpi with tip of apical segment darker. Punctures on head moderately sized, a few larger punctures inwards from eyes a little smaller than eye facets and about 4x diameter of adjacent punctures. Pronotum similarly punctate, systematic punctures relatively weak, smaller than eye facets. Interstrial punctures on elytra weak, verging on subobsolete, serial punctures also relatively small and weak, both a little stronger apically and laterally, on humeral angle the serial punctures are about 3x the diameter of adjacent punctures but both are small and relatively weak. Mesosternal keel moderately developed, ventral edge flat except for a well developed anterior protuberance.

Male: Genitalia variable in elongation, aedeagus usually relatively broad, narrowing to rounded point, collar closer to base than tip. Parameres relatively narrow, pointed. Male and female claws similar.

Distribution

Australian Capital Territory

Blundello Creek, ANIC; Canberra, SAMA.

New South Wales

Albury, ANIC; Ashfield, AM; Balranald, NMV; Berry, SAMA; Bogan River, AM; 20 mls SSW Bourke, SAMA; Collector, SAMA; Congo, ANIC; 9 km NNE Coonabarabran, ANIC; 14 km W Coonabarabran, ANIC; De Burghs Rng, AM; Deniliquin, ANIC; 37 km E Hay, SAMA; Illadulla, ANIC; Jenolan Caves, SAMA; Kenilworth, ANIC; North Sydney, NMV; Tooloom Plateau, UQIC; Wallacia, SAMA; Wilcannia, SAMA; 3 km S Wingellow, ANIC; Wingham Scrub, ANIC; Wootton, ANIC; Valery, ANIC.

Northern Territory

30 mls W Alice Springs, ANIC; Stanley Chasm, SAMA; 100 mls W Mt Olga, WAM; 30 km N Wauchope, ANIC; Yuendumu, SAMA.

Queensland

31 km NE Aramac, SAMA; Atherton, QDPIM; Babinda, UQIC; Brisbane, UQIC, SAMA; Bundaberg, ANIC; Byfield, ANIC; Cardstone, ANIC; Clermont, AM; Edungalba, ANIC; Funnell Creek, ANIC; 50 mls W Mackay, ANIC; Mt Coolum, ANIC; 9 mls S Stanthorpe, ANIC;

South Australia

Arkaba Creek, SAMA; 80 mls S Cooper Pedy, SAMA; 10 km SE Coward Springs, SAMA; Murray River, SAMA; Wintana Station, SAMA.

Victoria

Healsville, SAMA; Maffra, UQIC; Nathalia, SAMA; Portland, SAMA; 13 km SE Shepperton, ANIC; 14 km NW Violet Town, ANIC.

Western Australia

Nr Mt Gibson, WAM; 3 km E by N Newman, ANIC.

Remarks

A widespread and common species resembling a small *E. deserticola* and difficult to separate from light morphs of this species without reference to the male genitalia. Somewhat more strongly punctured than in most *E. deserticola*. In the North-east, *E. maculiceps* is sympatric with *E. weiri* and *E. pseudoweiri* which it closely resembles in general form. Both these species are a little more strongly punctured and have pale tips to their maxillary palpi and usually only a small central triangular area of black on the front of the head. However *E. maculiceps* with pale palpi and the central black portion on the front of the head reduced to a triangle, are not uncommon.

The male genitalia are variable in elongation, from a squatter form with the aedeagus quite curved in lateral view, with a strong apical pad and with only a small amount of structure apical to the pad, through to a more elongate form with elongate parameres, nearly straight aedeagus with a weak apical pad and a quite pronounced broadly triangular portion apical to the pad.

Some more strongly punctured specimens of *E. maculiceps* may approach weaker punctured specimens of *E. malabarensis*. In *E. malabarensis* the front of the head is nearly all black whereas in *E. maculiceps* the black area is seldom more than a third the width of the front of the head.

I have compared Australian specimens with the holotype, a paratype and five other specimens of *E. artensis* Fauvel from New Caledonia in IRSNB including two dissected males and consider that *E. artensis* is a junior synonym of *E. maculatus*.

Enochrus (Methydrus) malabarensis (Régimbart)

Philhydrus malabarensis Régimbart, 1903

Enochrus (Lumetus) malabarensis (Régimbart):
Knisch, 1924

Types

Enochrus malabarensis: Holotype. 'Make, Calicut Ind'; 'Philhydrus malabarensis Reg', MNHN.

Description (number examined, 37) Fig. 12

Length 2.5 mm – 4.1 mm. Broadly oval. Elytron and pronotum coloured as for *E. pseudoweiri*. Head black, areas in front of eyes light testaceous to about width of eye, central black panel 3–4x width of lateral light area. Ventral surface as for *E. pseudoweiri*, tips of maxillary palpi sometimes a little darker than rest of palpi. Punctures on head relatively strong, often approaching the size of eye facet, systematic punctures inwards from eye a little larger, sometimes hard to trace. Pronotum moderately to strongly punctured, systematic punctures often hard to trace. Punctures on elytra somewhat stronger towards apex and sides, approaching size of serial punctures which, as a consequence, may be difficult to distinguish. Mesosternal keel moderately developed, pronounced protuberance anteriorly, composed almost entirely of broad basal portion.

Male: Aedeagus relatively short, narrow, pointed with only slight apical pad, collar equidistant from tip and base. Parameres broad in basal half, narrow in apical quarter, inner edges almost straight, tips rounded. Proclaw rounded or weakly straightened strongly swollen at base, meso- and metac claws, rounded.

*Distribution***New South Wales**

Ashfield, AM; Bondi Heights, AM; Sydney, NMV, SAMA.

Northern Territory

Black Point Coburg Peninsula, ANIC; Coastal Plains Research Stn, ANIC; Crocodile Island, SAMA; Darwin, ANIC, SAMA; Groote Eyland, SAMA; Howard Springs, ANIC; Kakadu NP, ANIC.

Queensland

Bowen, SAMA; Brisbane, UQIC; Bundaberg, ANIC; Stewart River, SAMA.

South Australia

Billa Kalina Station, SAMA.

Remarks

The moderate size and strong dorsal punctation separate *E. malabarensis* from all other Australian

Enochrus. The punctation is strongest in specimens from the Darwin area where the systematic punctures on pronotum and elytra are virtually untracable. The punctures get weaker to the south where some specimens can approach the situation in the most strongly punctate *E. maculiceps*, *E. pseudoweiri* and *E. weiri*. The greater extent of black on the front of the head (the palc area reduced to the width of an eye) will separate *E. malabarensis* from these species where the black portion covers <1/3 of the head width. *Enochrus malabarensis* has the unusual combination of strongly black head with pale tips to the maxillary palpi.

The male genitalia of *E. malabarensis* differ from those of *E. maculiceps* in that the inner margin of the parameres are straight rather than sinuate to accommodate the apical pad on the aedeagus. Although the tip of the aedeagus in *E. malabarensis* is thickened dorsoventrally, it is not laterally expanded (to varying degrees) as in *E. maculiceps*.

The mesosternal keel is stronger than in *E. weiri* and *E. pseudoweiri* and most specimens of these species lack the pronounced anterior downward protuberance found in both *E. malabarensis* and *E. maculiceps* (Fig. 17). The genitalia of *E. weiri* is distinctive, that of *E. pseudoweiri* quite closely resembles *E. malabarensis* but has a shorter and thinner aedeagus.

Enochrus malabarensis differs from the two other strongly punctate Australian *Enochrus* (*E. eyrensis* and *E. samae*) by its smaller size, lack of black colour morphs, usually pale maxillary palpi, stronger punctation particularly on the head and the strong downward protuberance at the front of the mesosternal keel which is usually lacking in *E. eyrensis* and *E. samae*. *Enochrus malabarensis* has a generally more northern distribution than the other two species but overlaps with *E. eyrensis* on the east coast. The male genitalia readily separate the species (Figs 5, 12).

I have not seen the type of *E. malabarensis* (it is unavailable at this time) and have based my concept of this species on specimens identified by d'Orchymont from Sulawesi in IRSNB.

Enochrus (Methydrus) pseudoweiri sp. nov.*Types*

Holotype: ♂, '16°03'S to 16°05'S, 145°28'E, Cape Tribulation area, Qld., 21–28 Mar 1984, A. Calder and T. Weir'. ANIC.

Paratypes: All male. 4, 'Cardwell Rng, N.Q., 30.9.87, G.B. 'Q363'; 'J. G. Brooks Bequest 1976', ANIC; 2, '15°03'S, 145°09'E, 3 km NE of Mt Webb, Qld., 1–3 Oct. 1980, T. Weir', ANIC; 1, 'Whitfield Rg., Rd., ca. 486 m, Qld., 3.ii.1970, at light, J. G. and J. A. G. Brooks', ANIC; 1, '12°44'S, 143°17'E, 8 km E by N of Mt Tozer, Qld., 7 July 1986, T. Weir and A. Calder', ANIC; 2, McIvor Rv., 25 mls N Cooktown, N Qld, 6 May 1970, S. R. Curtis', one ANIC, one SAMA; 1, 'Australia, N Qld, Iron Rangc, 26–31.x.1991, Wood, Dunn and Hasenpusch', QDPIM; 1, 'Cow Bay, N of Daintree N Qld, 20–1 7–11 1984 1, C. Cunningham', QDPIM; 1, 'Cow Bay, N of Daintree, Qld., 27/7/82, C. Watts', SAMA; 4, 'Peach Ck, N Qld., 24/7/87, C. Watts', SAMA; 1, 'Cairns, C. J. Wild, Jan 91', QM.

Description (number examined, 33) Fig. 3

Length 3.0 mm – 3.6 mm. Oblong oval. Elytra testaceous to dark-testaceous, sutural region and serial punctures darker; small darker patch on humeral angles in many specimens. Pronotum dark testaceous centrally, widely lighter laterally. Head dark testaceous-black, frons area light testaceous except for small triangularly shaped dark area with apex often not reaching front of head, boundary between darker area and light areas indistinct, clypeus dark testaceous, ventral surface dark testaceous, appendages somewhat lighter towards extremities, maxillary palpi lacking darker tip. Head sparsely covered by small weak punctures, much smaller than facets of eyes, a few larger punctures inward from eyes about size of eye facet and 2–3x larger than adjacent punctures. Elytral punctures a little stronger, shallow. Serial punctures relatively weak, hard to trace laterally except on humeral angles where they are more distinct and 3–5x the diameter of adjacent punctures. Mesosternal keel strongly raised, ventral edge weakly convex, usually with a distinct anterior protuberance, broader basal portion making up most of keel with only a narrow thinner section in lateral view.

Male: Genitalia very stout to moderately stout overall. Aedeagus very slender, lacking terminal pad, collar nearer base than tip. Parameres broad, tips rounded. Proclaws curved, strongly swollen in basal half, more so than in female.

Distribution

Queensland

Cairns, ANIC; Cardstonc, ANIC; Cardwell,

ANIC; Cape Tribulation area, ANIC; 3km S by W of Cooktown, ANIC; 25mls N Cooktown, ANIC, SAMA; Cooktown, ANIC; 2mls N Kuranda, ANIC; 8km E by N of Mount Tozer, ANIC; 3km NE of Mount Webb, ANIC; Peach Ck, SAMA; 15km WSW South Johnstone, QDPIM; Whitfield Rg Rd, ANIC.

Northern Territory

Howard Springs, ANIC.

Remarks

Apart from the male genitalia and a tendency for the darker portion at the front of the head to be larger and more diffuse, I can find no difference between this species and *E. weiri* (see under *E. weiri*).

Enochrus (Methydus) samae sp. nov.

Types

Holotype: ♂, 'East Pomborneit, Vic. 24 km ESE Camperdown. Temporary pond, Aug. 1978–Feb. 1979, P.S. Lake coll.', ANIC.

Paratypes: 2 ♂, same data as holotype, ANIC; 2 ♀, '29.01°S, 167.57°E, Norfolk Island, Filmy Fern Walk, 14 Nov. – 2 Dec. 1984, I.D. Naumann ex ethanol', ANIC; 4 ♀, 4 ♂, 'Stonor, Tas: Lea', SAMA; 'Swansea, Tas., Jan. C. Watts', SAMA; 1 ♀, 1 ♂, '10 km S Robe S.A., 1/83, C. Watts', SAMA; 2 ♂, 'Grampians, Vic., 2.63, C. Watts', SAMA; 1 ♂, 'Chain of Ponds, S.A., December 1957, C. Watts', SAMA; 1 ♂, 'Mylor, S.A., Aug. 1958, C. Watts', SAMA.

Description (number examined, 47) Figs 9, 15

Length 4.0 mm – 5.0 mm. Oblong-oval. Elytra and pronotum dark-testaceous, quite broadly lighter at sides, dark area broken up with longitudinal rows of spots towards apex, front of pronotum often narrowly light-testaceous. Head dark-testaceous to black except for broad light-testaceous areas forward from eyes, leaving a central dark panel which is about the same width as one of the pale patches, boundary between the dark central panel and pale patches diffuse. Underside dark-testaceous, appendages only slightly lighter towards extremities, apical portion of apical segment of maxillary palpi darker. Punctures on head relatively strong, not much smaller than eye facet, a few larger punctures inward from eyes, about 3x the diameter of adjacent punctures; pronotal punctures on elytra a

little stronger than on pronotum, towards apex and laterally approaching size of stria punctures which are consequently not easily traced. Mesosternal keel moderately developed, triangular shaped, broader basal portion makes up most of keel.

Male: Aedeagus broad, well-marked terminal dorsal pad, collar nearer to base than to tip. Parameres with rounded tips. Male proclaws greatly swollen in basal half, strongly curved in apical half, female less swollen and more evenly curved.

Distribution

Australian Capital Territory

Black Mt., ANIC.

New South Wales

Norfolk Isl., ANIC.

South Australia

Chain of Ponds, SAMA; Mylor, SAMA; 10 km S Robe, SAMA.

Tasmania

George Town, SAMA; Stonor, SAMA; Swansea, SAMA.

Victoria

Grampians, SAMA; Hamilton, NMV; Lorne, SAMA; Otway Rngs., UQIC; East Pomborneit, ANIC.

Remarks

In general facies this species is very similar to *E. eyrensis* and at least in the South-east occurs sympatrically with it. The strong dorsal punctation and patterned head readily separates these two species from other *Enochrus* in the region. *Enochrus samae* differs from *E. eyrensis* in having rounded rather than hooked tips to the parameres and in a squatter mesosternal keel. This latter character is hard to use if comparative material is not available

***Enochrus (Methydrus) weiri* sp. nov.**

Types

Holotype: ♂, '12°44'S, 143°14'E, 3 km ENE of Mt Tozer, Qld., 28 Jun – 4 Jul 1986, T. Weir and A. Calder', ANIC.

Paratypes: All ♂. 1, '12°44'S, 143°17'E, 8 km E by N of Mt Tozer, Qld., 7 July 1986, T. Weir and A. Calder', ANIC; 1, '12°44'S, 143°14'E, 3

km ENE of Mt Tozer, Qld., 28 Jun – 4 Jul 1986, T. Weir and A. Calder', ANIC; 2, '12°43'S, 143°17'E, 9 km ENE of Mt Tozer, Qld., 5–10 July 1986, T. Weir and A. Calder', one ANIC, one SAMA; 1, 'Dejinghe Ck, N.Q., 3 mls SW of Yarrabah, 26.x.1966 E. Britton, R. Trumble', ANIC; 1, '16°03'S to 16°05'S, 145°28'E Cape Tribulation area, Qld., 21–28 Mar 1984, A. Calder and T. Weir', ANIC; 1, 'Australia, N Qld., Cow Bay N of Daintree R, 13.ix.1990, Cunningham and DeFaveri', QDPIM; 1, 'Australia, N Qld Cow Bay N of Daintree R, 14.xii.1987–6.i.1988, Storey and Cunningham', QDPIM.

Description (number examined, 18 with male genitalia extracted) Fig. 8

As for *E. pseudoweiri* except for male genitalia.

Male: Aedeagus broadest in middle, tapering to a point, lacking any terminal dorsal pad. Tips of parameres truncated, weakly bifid.

Distribution

Known only from type localities on Cape York in North Queensland.

Remarks

A tropical species known only from the Queensland east coast, north of Cairns. I have found no reliable way to separate this species and *E. pseudoweiri*, with which it is sympatric over most of its range, other than by the distinctively different male genitalia. These species can also be readily confused with *E. maculiceps* and with small brown colour morphs of *E. deserticola* which also occur in the region. The virtual absence of black on the front of the head and pale tips to the maxillary palpi will separate them from most examples of these species. Most *E. weiri* lack or have only a small downward protuberance at the front of the mesosternal keel whereas most *E. maculiceps* have it well developed. The differently coloured head and weaker dorsal punctures will readily separate *E. weiri* from the similarly sized *E. malabarensis*.

ACKNOWLEDGMENTS

I thank the curators of the collections listed earlier for allowing me ready access to specimens in their care: Ms D. Churches typed the manuscript, Mr R. Gutteridge prepared the figures, Mrs M. Anthony and Mrs J. Evans helped with the library references and Dr E. Matthews helped improve the manuscript.

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RECORDS OF THE SOUTH AUSTRALIAN MUSEUM

VOLUME 30 PART 2

JANUARY 1998

ISSN 0376-2750

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